

CYTOPALYNOLOGICAL STUDY OF AFRICAN HEDYOTIDEAE (RUBIACEAE)¹

BY WALTER H. LEWIS

Missouri Botanical Garden and Department of Botany, Washington University,
St. Louis, Missouri

In the Americas only five or six genera are known in the rubiaceous tribe *Hedyotideae* (Lewis 1962a, 1965), but in Africa, south of the Sahara and in adjacent islands, at least thirty are found. A cytopalynological study of these genera was undertaken in an attempt to describe their chromosomal complements and pollen forms in the tribe's center of diversity and to compare them with those from the Americas. Such a study should better characterize the tribe in these continents and should develop an understanding of major phylogentic trends in the whole tribe *Hedyotideae*. Evidence from these disciplines might also improve present classifications by confirming or rejecting certain intergeneric realignments which in the past have been proposed for African members of the tribe.

The genera are discussed under four groupings, three with known chromosome numbers, and the fourth unknown. Procedures, materials and results of the chromosomal study are summarized in Appendix 1. Species studied palynologically, together with the techniques involved, are given in Appendix 2. Author citations for species and lower taxa are given in the appendices when these have been studied cytopalynologically.

I. BASIC CHROMOSOME NUMBER $X = 9$.

AGATHISANTHEMUM Klotzsch

An African genus consisting of six species of which three are restricted in distribution, *Agathisanthemum* is said by Bremekamp (1952) to show a close relationship with the Asian section *Diplophragma* W. & A. of *Hedyotis* L., particularly in its form of capsular dehiscence. Among the African members of the *Hedyotideae* he suggested a close affinity with *Dibrachionostylus*.

The chromosomes of *A. bojeri* and *A. globosum* are small and based on $x = 9$ and resemble those of *Oldenlandia* and a number of allied genera.² Both subspecies³ of *A. bojeri* are diploid ($n = 9$) and *A. globosum* is tetraploid ($n = 18$).

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²Whenever it is suggested that taxa are related or allied, it means that they are morphologically similar over a large range of structures (often including palynological and chromosomal); nevertheless the relationship remains hypothetical.

³On discussing the use of subspecies as an infraspecific category, particularly in answer to remarks by van Steenis (*Flora Malesiana*, ser. 1, **5**: 167-234. 1957), Bremekamp (*Proc. K. Ned. Akad. Wetensch.*, ser. c, **62**: 107. 1959) noted that he had only once used the category and this in the genus *Acanthus*. Clearly, however, the subspecies he described for *A. bojeri* (1952) are a second exception.

ANN. MISSOURI BOT. GARD. **52**(2): 182-211. 1965.

The pollen of *A. bojeri*, *A. globosum* and *A. quadricostatum* is colporate with apertures consisting of long, narrow colpi and compound ora (cf. Lewis, 1965). These ora consist of an os, designated type A, which is delimited by a very thin layer of nexine in the equatorial zone and surrounded by a much thickened layer of nexine, and a second os, designated type B, which is pore-like and surrounded by a distinct nexinous margin. The type A os is usually in the shape of an elongated diamond, whereas the type B os is circular and ca. $2.7\ \mu$ in diameter (Fig. 16f). The grains are 3- to 4-aperturate, subspheroidal and vary in size from only $20\ \mu$ (E) $\times$ $19.3\ \mu$ (P) for the long-styled flowers of *A. bojeri* to $29.3\ \mu \times 26.7\ \mu$ for the short-styled flowers of *A. quadricostatum*. Pollen of short-styled flowers of *A. bojeri* is slightly larger ($21.3\ \mu \times 22.7\ \mu$) than that of long-styled ones, but pollen from both floral types of *A. bojeri* (2x) is smaller than the pollen from the isostylous, tetraploid species *A. globosum* ($26.9\ \mu \times 26.7\ \mu$). The sexine of all species is thin (ca. $1\text{--}1.4\ \mu$) and finely reticulated.

The aperture morphology for *Agathisanthemum* is the same as that known for the monotypic genus *Lelya*, but such a specialized aperture has been described for a majority of the North American species of *Hedyotis* subg. *Edrisia* (Lewis, 1965). This kind of aperture is not found in the Asian members of *Hedyotis* thought to be closely allied to *Agathisanthemum* nor in *Dibrachionostylus*.

AMPHIASMA Bremek.

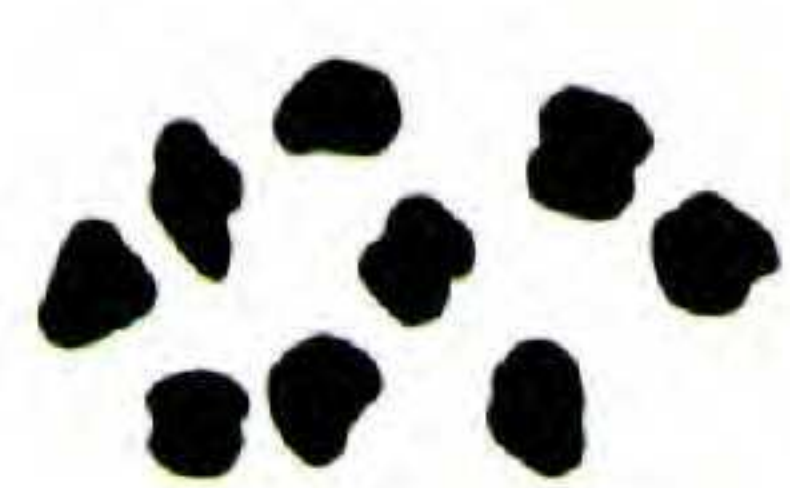
A genus erected by Bremekamp (1952) to include those species formerly recognized under *Oldenlandia* having few, dorsiventrally flattened seeds and cylindrical stipular sheaths, *Amphiasma* consists of eight species endemic to Africa. All are restricted in distribution and none is well collected. Bremekamp noted that *Amphiasma* is most nearly allied to *Eionitis*, *Lelya* and *Oldenlandia*.

The chromosomes of *Amphiasma* are small and based on $x = 9$. An undetermined species from South West Africa is diploid and *A. merenskyanum* is tetraploid.

The pollen of *A. benguillense* and *A. merenskyanum* is small ($26.7\ \mu \times 20\ \mu$ and $25.3\ \mu \times 24\ \mu$, respectively), subspheroidal, 3-colporate with long, narrow colpi and simple, type A ora distinctly diamond-shaped (Fig. 16b), and with a thin sexine (ca. $1.2\ \mu$ in thickness) having fine or medium-fine reticulations. This is indistinguishable from the pollen of the majority of *Oldenlandia* species in the structure of the aperture, in pollen size and shape, and in the characteristics of the wall.

CONOSTOMIUM Cuf.

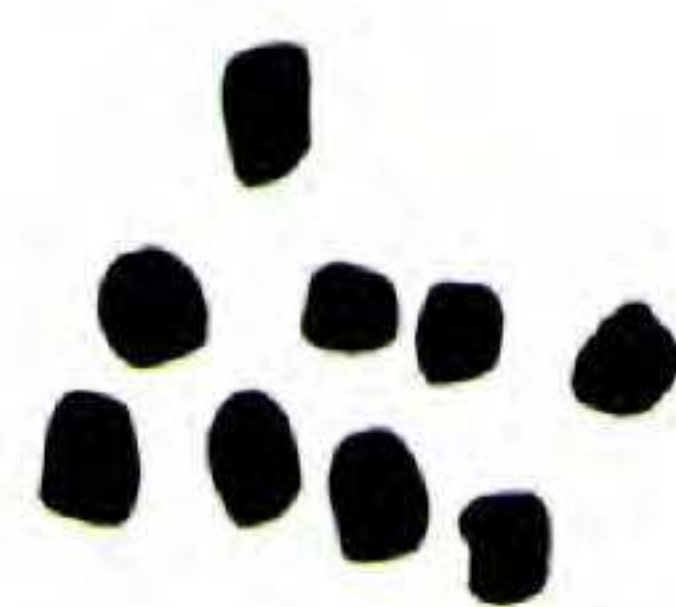
Nine species of *Conostomium*, all endemic to Africa, are recognized under three subgenera. Bremekamp (1952) distinguished the genus from its nearest allies (*Oldenlandia*, *Kohautia*, *Pentanopsis*) by the long cylindrical corolla tube with included anthers and typically exserted styles, large fruit and granulated basal walls of the testa. Emphasizing the distinctiveness of the pollen grains he describes them as “. . . larger than in the other genera belonging to this circle of affinity, they



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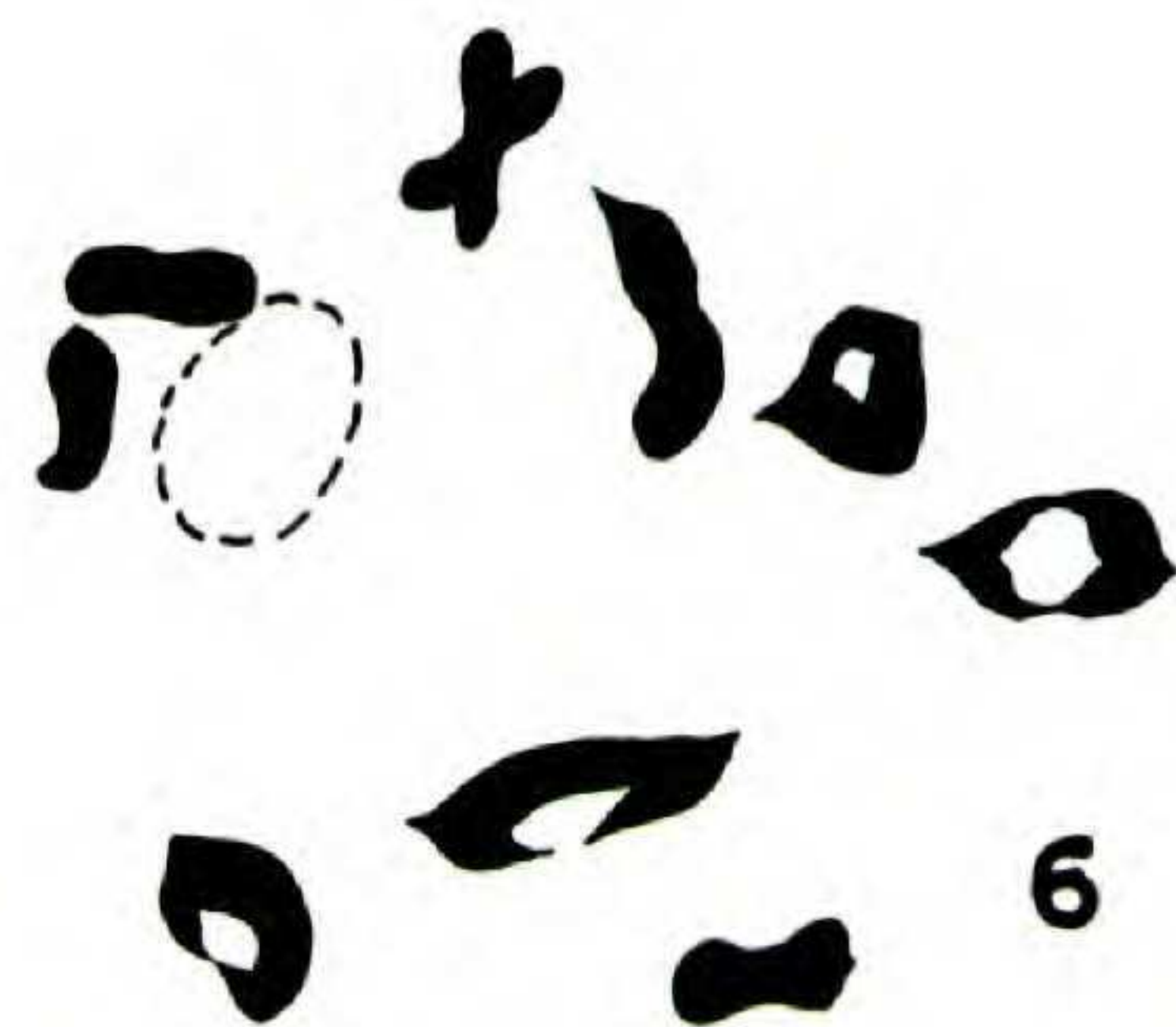
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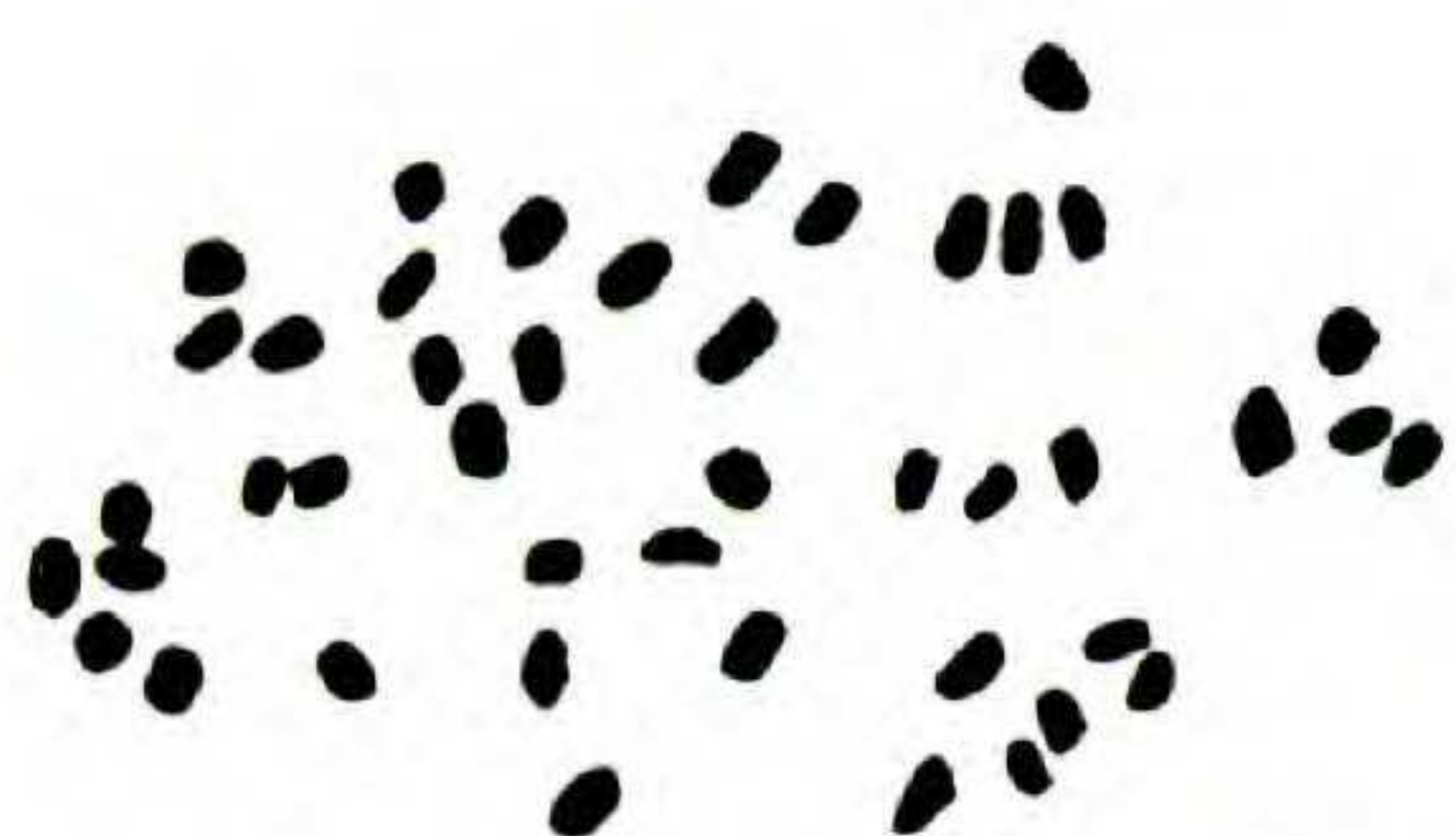
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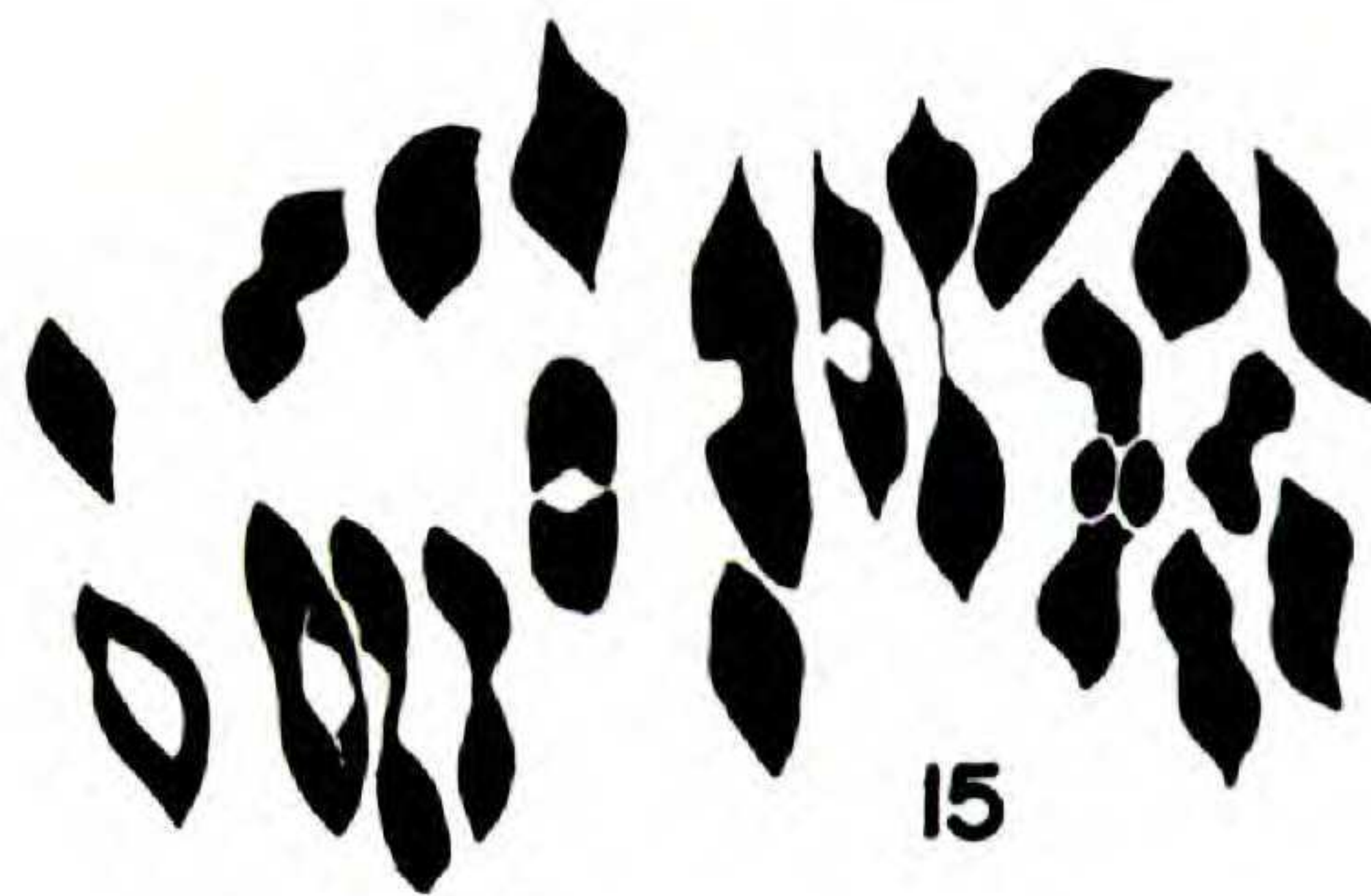
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possess a very thin wall, and they are not colporate but porate. The pores, moreover, are enclosed between a couple of short, easily staining bars, one at the top and the other one at the base of the pore."

The chromosome complements of *C. kenyense* (4x) and *C. natalense* (2x) are based on $x = 9$ and the chromosomes are small, e.g., metaphase II chromosomes of *C. natalense* average only 1.1μ in length (Fig. 1). This is comparable to the chromosome sizes for *Kohautia cynanchica* (Fig. 3) and *Oldenlandia capensis* (Fig. 4) at the same stage of meiosis.

Pollen representative of the three subgenera of *Conostomium* is medium in size ($29.3 \mu \times 28 \mu$ for *C. kenyense* to $39.4 \mu \times 40 \mu$ for *C. quadrangulare*), subspheroidal, 3-colporate, with colpi medium (13μ) to short (8μ) in length, narrow to rather broad (3.8μ) and simple type A ora, 2.7 - 6.7μ high, delimited vertically by thick concentrations of nexine which are horizontally incomplete (Fig. 16i, j). The sexine is thin (ca. 1μ) to thick (ca. 3μ) with fine to coarse (in *C. natalense*) reticulations, excepting the pollen of *C. quadrangulare* which is verrucose. The nexine is $\frac{2}{3}$ the thickness of the sexine, although when adjacent to the ora it is about twice as thick.

Bremekamp (1952) described the pollen from seven species of *Conostomium* as porate, but of the four species examined in this study I was able to measure distinct colpi. The colpi may, however, be short and since Bremekamp apparently observed non-acetolyzed pollen, a brevicolpate condition could easily be overlooked. Bremekamp's description of the pores enclosed by "two bars" does characterize the ora of *C. natalense* (subg. *Conostomium*) and *C. quadrangulare* (subg. *Hockstetteria*) as illustrated in Fig. 16j. These crescent-shaped nexinous thickenings delimiting the upper and lower limits of each os are unique among the pollen studied. It does not describe the pollen of species in the subg. *Beckia* (*C. kenyense*, *C. longitubum*) for which the nexinous thickenings are coarsely triangular-shaped (Fig. 16i). These are not unlike those for the species of group 1 in *Hedyotis* subg. *Edrisia* (Lewis, 1965) and for some species of African *Oldenlandia* (Fig. 16c).

According to Bremekamp (1952), the pollen for *Conostomium* is larger than that of other genera belonging to this "circle of affinity." The mean size for three of the species I examined was $29.5 \mu \times 29.3 \mu$ with the pollen of *C. quadrangulare* considerably larger ($39.3 \mu \times 40 \mu$). Bremekamp's diagram (1952:295) of the pollen of *C. longitubum* measures less than 20μ in diameter, even though his size

Fig. 1-15. Chromosomes drawn with the aid of a camera lucida originally at $\times 2800$, reduced by ca. $\frac{1}{4}$ in reproduction. Fig. 1. *Conostomium natalense*, Lewis 6332, $n = 9$ (1 set metaphase II). Fig. 2. *Kohautia grandiflora*, Lewis 5997, $n = 9$. Fig. 3. *K. cynanchica*, Lewis 6313, $n = 9$ (1 set metaphase II). Fig. 4. *Oldenlandia capensis*, Lewis 6210, $n = 9$ (1 set metaphase II). Fig. 5. *O. cephalotes*, Lewis 6314, $n = 9$. Fig. 6. *O. duemmeri*, Lewis 6018, $n = 9$. Fig. 7. *O. echinulosa*, Lewis 6091, $2n = 18$. Fig. 8. *O. herbacea* var. *goetzii*, Lewis 6228, $n = 9$. Fig. 9. *O. saxifrigoides*, Hemming 1673, $2n = 18$. Fig. 10. *Pentodon pentandrus*, Lewis 6027, $n = 9$. Fig. 11. *Otomeria elatior*, Lewis 6215, $n = 10$. Fig. 12. *Pentas longiflora*, Lewis 5962, $n = 10$. Fig. 13. *P. zanzibarica* var. *intermedia*, Lewis 6005, $n = 10$. Fig. 14. *Manostachya staelioides*, Lewis 6128, $2n = 44$. Fig. 15. *Pentanisia ouranogyne*, Lewis 5965, $n = 20$.

descriptions for seven species average $23.3\ \mu$ to $25\ \mu$. Providing that *Oldenlandia* is considered a genus belonging to this circle of affinity, then his measurements of pollen are very similar to a majority of *Oldenlandia* species and even the larger sizes recorded in this study from acetolyzed grains are also known for *O. herbacea*, *O. monanthos*, *O. rupicola* and others. They are also similar in size to the grains of *Pentanopsis fragrans* Rendle, but larger than those for all species of *Kohautia* studied.

Finally, Bremekamp (1952) described the pollen of *Conostomium* as very thin-walled and although such a sexine is typical of members of the subg. *Beckia*, all species in the other subgenera are thick-walled, as thick as any known for African members of the *Hedyotideae*.

Although the distinctiveness of the pollen for *Conostomium* has been incorrectly overemphasized, it does illustrate several unique features, the most striking of which is the brevicolpate condition characteristic of species in the subgenera *Conostomium* and *Hochstetteria*. These species also have pollen with unusual crescent-shaped nexinous thickenings partially surrounding their ora. Moreover, the verrucose sexine known for *C. quadrangulare* is unique among the pollen of members of this tribe in Africa.

DIBRACHIONOSTYLUS Bremek.

The monotypic genus *Dibrachionostylus* was separated from *Oldenlandia* largely on the basis of capsule dehiscence, viz., both loculicidally and septicidally for the former and only loculicidally for the latter. Bremekamp (1952) closely associated *Dibrachionostylus* with *Agathisanthemum* because of their similar dehiscence.

The chromosomes of *D. kaessneri* are small with $n = 9$. The pollen is medium-small ($26.7\ \mu \times 24.7\ \mu$), subspheroidal, 3-colporate with long, narrow colpi and type A ora, $4\ \mu$ high and indefinite horizontally, with $\pm$ thin sexine (ca. $1.5\ \mu$ thick) having medium reticulations and with nexine about $1/2$ as thick as the sexine.

In aperture morphology *Dibrachionostylus* differs markedly from the more specialized form known for *Agathisanthemum*, but the aperture is similar to that described for *Amphiasma*, *Oldenlandia* and *Pentodon*.

KOHAUTIA C. & S.

Forty-eight species of *Kohautia* from continental Africa are described (Bremekamp, 1952), with perhaps 12 additional species known to Madagascar and southern Asia. *Kohautia* is distinguished from its closest African allies by a cylindrical corolla tube having a slightly widened upper region containing sessile anthers, while the short-style is usually included in the narrow, lower part of the tube. The monomorphic, short-styled condition is, with the exception of a few individuals of *Conostomium*, unique among the African members of the tribe. The same floral morphology is known for some species of *Hedyotis* subg. *Edrisia* indigenous to the southern United States (Lewis, 1962a). As noted by Bremekamp (1952), pollen grains are 3- to 8-colporate and small and as such differ from the grains known for *Oldenlandia* and other allied African genera.

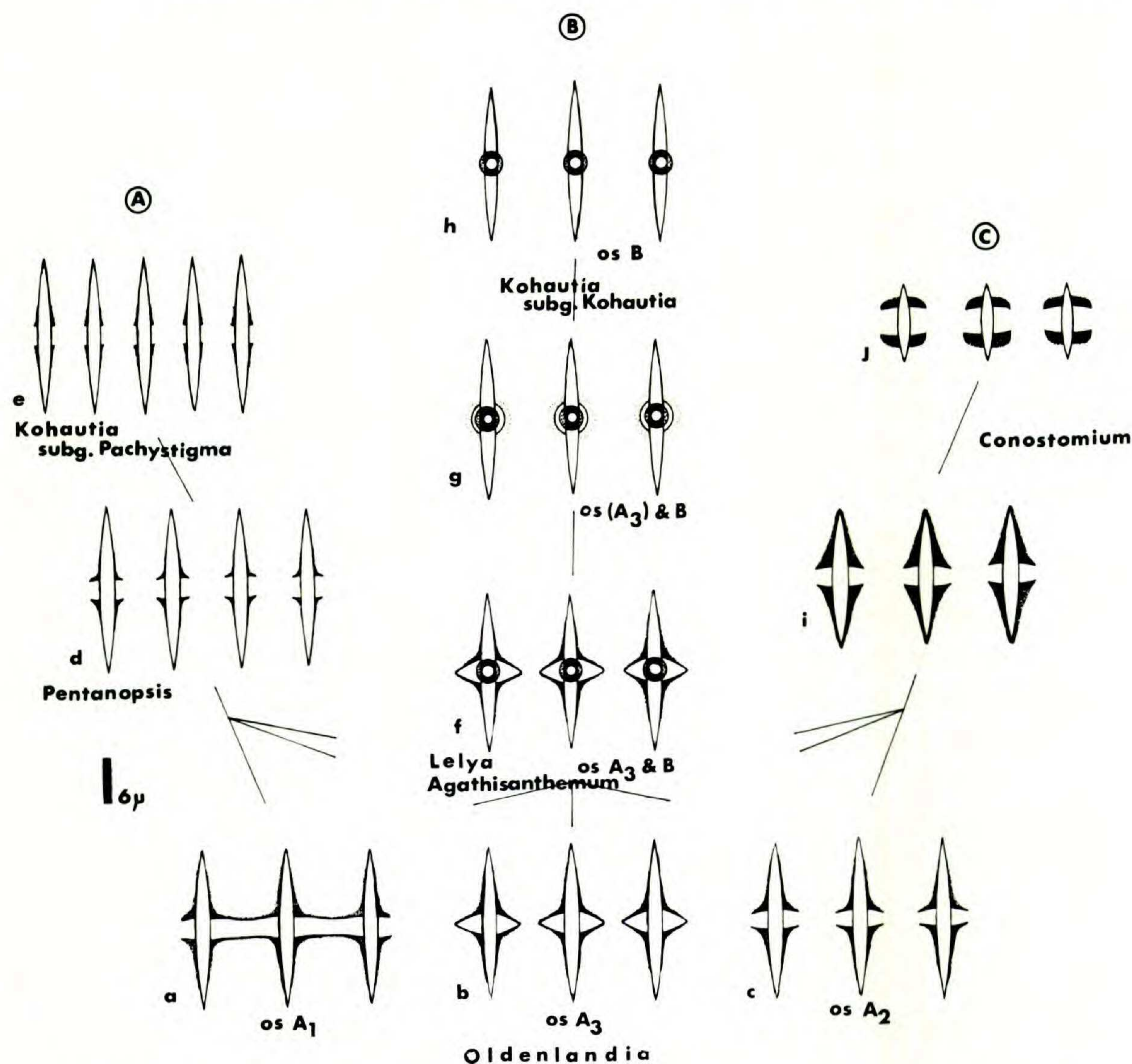


Fig. 16. Diagrammatic representation of pollen aperture types for *Oldenlandia* and its allies in Africa. Three lines of modification lead from a 3-aperturate condition having long colpi and simple, type A ora to: (A) 4- and 5-aperturate types (up to 8, not illustrated) in closer proximity with an associated decrease in nexinous thickenings and a consequent weakening of *os A₂*; (B) compound ora with distinct oral types *A₃* and B, to a very reduced *A₃*, to its absence and presence only of *os B*; (C) colpi medium in length and to a brevicolpate condition associated with a nexinous concentration surrounding the *os*. Fig. a-c - All species of *Oldenlandia* and many *Hedyotideae* illustrating kinds of ora, type A. Fig. d - *Pentanopsis*, some *Kohautia* species. Fig. e - Most species of *Kohautia* subg. *Pachystigma*. Fig. f - *Agathisanthemum*, *Lelya*. Fig. g - *Nesohedyotis*, some species of *Kohautia* subg. *Kohautia*. Fig. h - Some species of *Kohautia* subg. *Kohautia*. Fig. i - *Conostomium* subg. *Beckia*. Fig. j - *Conostomium* subg. *Conostomium* and subg. *Hochstetteria*.

The chromosome number for *K. senegalensis* C. & S. was reported by Hagerup (1932) from west African collections as $2n = 18$ and for *K. aspera* by Raghaven and Rangaswamy (1941) from India as $n = 18$. To these counts are added those for eight other taxa, as well as a verification of the number for *K. aspera* from an Ethiopian collection. All species have a basic complement of $x = 9$ consisting of either small or medium-small chromosomes. The chromosomes for *K. cynanchica* (Fig. 3) average approximately 1.1μ long and are similar in size to those illustrated for *Conostomium natalense* (Fig. 1) and *Oldenlandia capensis* (Fig. 4). The bivalents

of *K. grandiflora* each have chromosomes averaging ca. 2 μ in length (Fig. 2) and resemble those of *Oldenlandia duemmeri* (Fig. 6). Diploid and tetraploid species are common, but only *K. virgata* was found to be hexaploid. Intraspecific chromosomal races were not observed, but otherwise the chromosomal pattern for *Kohautia* resembles that known for *Oldenlandia*.

Pollen from 20 species of *Kohautia* was studied which represents slightly more than $\frac{2}{5}$ of the described African species. Of the remainder, $\frac{2}{5}$ are known from only the type collection or from this and one other specimen. The grains are small (12 $\mu \times 12.8 \mu$ to 22.7 $\mu \times 21.3 \mu$), subspheroidal, usually prolate or oblate-spheroidal, commonly 3- to 5-, rarely 6- to 8-, aperturate with size correlated with aperture number, viz., smallest grains 3-colporate, those having a polar axis 18 μ or more in diameter always 4- or more colporate. The colpi are long and narrow, occasionally constricted equatorially and with smooth membranes. The ora are simple or infrequently compound.

Pollen of the subg. *Pachystigma* consists of type A ora, either obscure laterally or rarely synclinorate. Pollen of the subg. *Kohautia* possesses type B ora which are usually circular (ca. 1.4 μ), thinly crassimarginate with the margin occasionally surrounded by a hallow-like area of thin nexine, thereby resembling compound ora. The sexine is ca. 1 μ thick, simplibaculate, usually medium to finely reticulated in the subg. *Kohautia* and is usually coarsely reticulated in the subg. *Pachystigma*.

Palynologically the species of *Kohautia* divide into two distinct groups corresponding exactly to a subgeneric classification proposed by Bremekamp (1952) on other evidence. The distinction of aperture types is universal among the species examined. Moreover, different subgeneric tendencies exist for pollen size, aperture number and certain exine features. These are summarized as follows:

Subg. *Kohautia* (based on 14 species).

- (1) simple os, type B, occasionally surrounded by an area of thin nexine (compound os).
- (2) smaller grains, mean size 16.9 $\mu \times 16.1 \mu$.
- (3) apertures typically 3 or 4, less commonly 5, very rarely 6.
- (4) usually thin, finely reticulated sexines.

Subg. *Pachystigma* (based on 6 species).

- (1) simple os, type A, obscure horizontally or rarely synclinorate.
- (2) larger grains, mean sizes 20.8 $\mu \times 19.9 \mu$.
- (3) apertures typically 4 to 5, infrequently and never exclusively 3, less commonly 6 to 8.
- (4) somewhat thicker, coarsely reticulated sexines.

I have noted that some North American species of *Hedyotis* possess a floral morphology similar to that of all described species of *Kohautia*. These American species also have in common with the subg. *Kohautia* a simple, crassimarginate os (type B). This parallelism is striking, for among the pollen of all Afro-American species of the *Hedyotideae* examined, only these two groups have such apertures. The species from the two continents differ by a number of important characters (e.g., seed morphology) so that the taxa are probably only of distant relationship.

The specialized parallelisms in both floral and pollen morphology do, however, suggest a genetic affinity of some significance (cf. Cronquist, 1963).

Pollen apertures of some species of the subg. *Kohautia* possess a vague, nexinous thin area adjacent to the margin of the os. This suggests an intermediate form between the clearly defined nexinous thin region as found in *Agathisanthemum*, *Lelya* and many North American species of *Hedyotis*, and the $\pm$ evenly thickened nexine adjacent to the os B of most species of the subg. *Kohautia*. These oral types are illustrated in Fig. 16g, h.

The absence of a crassimarginate os (type B) for all species examined in the subg. *Pachystigma* identifies the pollen of this group. Even the type A os is very obscure ventrally for the nexinous thinnings adjacent to the colpus measure only ca. 0.5 μ in thickness. Horizontally the ora extend for about 1-2 μ on each side of the colpus, but, excepting *K. cuspidata*, these extensions are difficult to observe. For *K. cuspidata* the ora are weakly continuous, but these often fade because of reduced nexinous concentrations away from the colpi. Furthermore, there is an increase in the average number of apertures per grain which brings the apertures closer. These aperture conditions in species of the subg. *Pachystigma* represent a second line of development for the pollen of *Kohautia* (Fig. 16d, e).

With the exception of the monotypic genus *Pentanopsis* all species of *Kohautia* can be readily separated by their pollen from those of *Oldenlandia* and all other African taxa in the tribe *Hedyotideae*.

LELYA Bremek.

The monotypic genus *Lelya* was erected by Bremekamp (1952) for plants having thick, woody-walled, conical beaked capsules which are tardily dehiscent and few seeded.

Among a group of unnamed *Oldenlandia* at the British Museum, I noted the type of *Spermacoce prostrata* R. Good (J. Bot. **65** (suppl. 2): 42. 1927). Good observed that "this species is very unlike any other member of the genus known to me in its general habit, but the structure of the flowers and fruit shows that it is a *Spermacoce*." On dissecting one fruit from the type specimen I found a total of eight angular seeds, not Good's "loculis 1-ovulatis." The fact that the plant is a member of the tribe *Hedyotideae* rather than a member of the *Spermacoceae* had already been recognized by Gilleland, for in this folder was a sheet annotated as an *Oldenlandia* named after the collector Jelf (Jelf 20, Fort Roseberry, N. Rhodesia) and signed H. B. G. This new epithet is also pencilled on Good's type, although to my knowledge it remains unpublished. The specimens are, in fact, *Lelya osteocarpa* Bremek., which must become *Lelya prostrata* (R. Good) W. H. Lewis, comb. nov. (*Spermacoce prostrata* R. Good, J. Bot. **65** (suppl. 2): 42. 1927; *Lelya osteocarpa* Bremek., Verh. K. Ned. Akad. Wet., Afd. Natuurk., ser. 2, **48**: 181. 1952). The holotype is from ANGOLA: Cuanza Norte District, near Capijango, near Lucala, Gossweiler 7385, 5 Jan. 1918 (BM). Two varieties are recognized: a pubescent form, *L. prostrata* (R. Good) W. H. Lewis var. *prostrata*, and a glabrous form, *L. prostrata* var. **angustifolia** (Bremek.) W. H. Lewis, comb. nov., based on *L.*

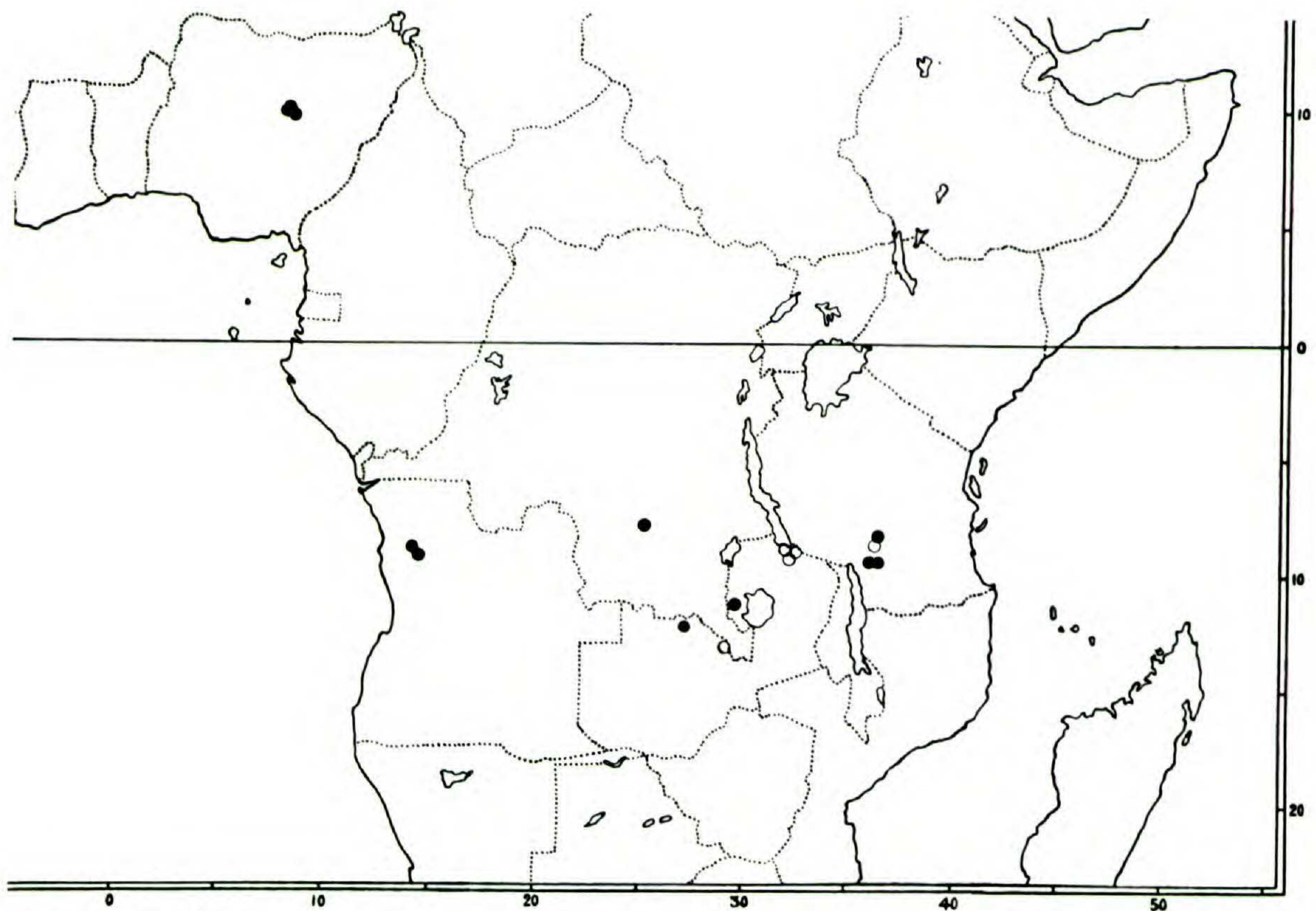


Fig. 17. Distribution of *Lelya prostrata* var. *prostrata* (•) and var. *angustifolia* (○).

osteocarpa var. *angustifolia* Bremek. (Verh. K. Ned. Akad. Wet., Afd. Natuurk., ser. 2, **48**: 183. 1952).

Bremekamp (1952) recorded the genus from the Congo (Léop.), Nigeria, N. Rhodesia and Tanganyika. Additional collections are now reportable from these countries, together with the first records from Angola as given below. The known distribution (Fig. 17) is discontinuous, which may be due to incomplete collecting or the preference of the species for savannahs and plateau around 1,000 m. generally subject to fires or to both.

All individuals on the type sheet of *L. prostrata* var. *angustifolia* are subglabrous and have very narrow leaves. However, the subglabrous plants considered here under var. *angustifolia* rarely have leaves as narrow as those known for the type collection. The stems of plants collected by Fanshawe (F361) and Richards (2049) are more pubescent than is typical of the var. *angustifolia*, but the leaves, ovaries and corollas are glabrous. This variety is common in northeastern N. Rhodesia while the var. *prostrata* is more prevalent elsewhere.

L. prostrata var. *prostrata* (additional to Bremekamp, 1952). ANGOLA. Cuanza Norte Dist.: near Capijango, near Lucala, Gossweiler 7385 (BM, holotype); Lamba Caju, Gossweiler 8488 (BM). NIGERIA. Plateau Prov.: Heipang, Keay et al. FHI 37612 (K); Werran, collector unknown, 27 Apr. 1946 (K). N. RHODESIA. Northern Prov.: Fort Roseberry Dist., Fort Roseberry, Jelf 20 (BM). TANGANYIKA. Southern Highlands Region: Iringa Area, 4.5 miles N.E. of John's Corner, Lewis 6067 (K, MO, US).

L. prostrata var. *angustifolia* (additional to Bremekamp, 1952). N. RHODESIA. Northern Prov.: Abercorn Dist., 1 mile S. of Abercorn, Lewis 6119 (K, MO, US); ca. 5 miles S. of Abercorn, Greenway & Brenan 8233 (K); Mpulungu, Richards 2019, 2049 (K); road to Ningi Pans, Richards 13161 (K); Lunzua Protected Forest Area, Lawton 442 (K); Western Prov., Ndola, Fanshawe F361 (K).

Lelya prostrata is a tetraploid species ($n = 18$) with small chromosomes. The pollen is medium small ($26.6 \mu \times 24 \mu$), subspheroidal, 3- to 4-aperturate with long, narrow, equatorially constricted colpi and compound ora consisting of type A ora, either diamond-shaped or occasionally $\pm$ synclinorate to ca. 3μ high, and type B ora which are small (2μ), circular or lolongate, and surrounded by a thin margin which is less than 1μ in thickness. The sexine is about 2μ thick, medium to finely reticulated and the nexine is $\frac{2}{3}$ as thick as the sexine.

The same kind of aperture has been found for *Agathisanthemum* and for some North American species of *Hedyotis* except that the type B os for *Lelya* is much more delicate (Fig. 16f). Like *Agathisanthemum*, the apertures may also number more than three per grain. By having compound ora, the pollen of *L. prostrata* differs from all known species of *Oldenlandia*; for the latter, ora are invariably simple.

OLDENLANDIA L.

The pantropical genus *Oldenlandia* is common throughout Africa south of the Sahara where 61 species have been reported (Bremekamp, 1952). A number of these are poorly known and some are of questionable validity (cf. Hepper, 1963; Lewis, 1964) but, regardless of these, the genus in Africa is represented by more species than in all other tropical areas combined. Africa is certainly the center of morphological diversity for the genus and there is strong evidence that the dispersal of the most widespread (and type) species, *O. corymbosa* L., was from central-east Africa with migration in two directions: first to southern Asia and the western Pacific, and then to western Africa and the Americas (Lewis, 1964). This example might also be indicative of the origin and pathways of migration for the genus as a whole.

Chromosome numbers for 23 species, representing 10 of the 16 described subgenera, are listed in Appendix 1. Excepting the counts for four species, all are new reports for *Oldenlandia*. Of the four, the number for *O. lancifolia* ($n = 18$) verifies that recorded by Lewis (1962b) from Mexican material, the tetraploid count ($n = 18$) for *O. capensis* confirms the reported number of Hagerup (1932) from a west African collection and the count from Indian material for *O. pumila* (as *O. crystallina* Roxb.) ($n = 9$) by Raghaven and Rangaswamy (1941) is verified by counts for material originating from Hyderabad and Uganda. The diploid, tetraploid and hexaploid numbers obtained for *O. corymbosa* are discussed in detail elsewhere (Lewis, 1964).

The basic chromosome number for all species of *Oldenlandia* s. s. examined is $x = 9$. In Africa the frequency of diploid species is 48% of this total. Tetraploids account for 26%, whereas 26% of the species were found to have more than one euploid race. These results are summarized in Table 1 together with the known data for related species in *Hedyotis* (Lewis, 1962a; Lewis & Terrell, 1962). For species in the latter genus, infraspecific euploidy totals 28%, almost identical in frequency and kind as in the African species of *Oldenlandia*. Inter- and infra-specific aneuploidy, currently unknown for the African species, is also widespread for the American species. It appears that numerical chromosomal changes are im-

Table 1. Frequency of euploidy and aneuploidy in African *Oldenlandia* and North American *Hedyotis* subg. *Edrisia*.

Chromosomal composition of species		Frequency (%)	
		Africa (23 spp.)	N. Am. (25 spp.)
Diploid		48	64
Tetraploid		26	8
Diploid and tetraploid		17.5	20
Diploid and 2 polyploid races		8.5	4
Tetraploid and hexaploid		0	4
Total infraspecific euploidy		26	28
Basic aneuploid series:	$x = 6$	0	16
	$x = 7$	0	8
	$x = 8$	0	16
	$x = 9$	100	4
	$x = 11$	0	36
	$x = 13$	0	20
Intraspecific aneuploidy		0	8
Species with 1 chromosomal race		74	64
Species with 2 or more races (euploid and aneuploid)		26	36

portant factors in the evolution of the species known for each group, by euploidy in both, but by aneuploidy only among the North American species.

The mitotic chromosomes of *O. echinulosa* measure ca. 1.1 μ in length (Fig. 7) and those of *O. saxifrigoides* ca. 1.1-1.3 μ (Fig. 9). The meiotic chromosomes in metaphase II of *O. capensis* (Fig. 4) also approach these lengths and as anticipated the bivalents illustrated for *O. cephalotes* (Fig. 5) and *O. herbacea* var. *goetzii* (Fig. 8) average twice as long. The bivalents of *O. duemmeri* (Fig. 6) suggest chromosomes 1.2-2.3 μ long, or slightly longer than those for the others. However, all chromosomes for the species of *Oldenlandia* examined would be considered $\pm$ small and, in this regard, are similar to those for all other genera having a basic complement of $x = 9$.

Among the African species of *Oldenlandia* with more than one chromosomal race, four are isostylous and each exhibits a strong weedy tendency. Another species, *O. monanthos*, is not a marked apocrat but the species is heterostylous, while the widespread *O. herbacea* is known with three diploid isostylous varieties and a tetraploid variety which is heterostylous. These data suggest first, that autopolyploidy might be advantageous to a species adapting to new environmental niches and conditions in the tropics. A study of weeds, taking into account chromosomal differences, might lead to an important conclusion regarding the role of autopolyploidy in the success of many pantropical species. A strong correlation certainly exists in *Oldenlandia* between some of the weediest species such as *O. corymbosa*, *O. herbacea* and *O. capensis*, and the occurrence of infraspecific tetraploidy, and the hexa-

ploidy. A second correlation is suggested by these data between the occurrence of heterostyly and autopolyploidy. In addition to the species cited from Africa, all seven species from North America with more than one euploid race are heterostylous. Why such a correlation should exist is at present unknown.

Pollen grains of *Oldenlandia* are small to medium in size ($21.3\ \mu$ to $32\ \mu \times 19.3$ to $30.5\ \mu$), subspheroidal (2-)3- (4-5-) aperturate with long, narrow colpi and simple type A ora, 2.5 - $5\ \mu$ high. These have definite diamond-shaped horizontal limits; less commonly the ora are laterally indefinite or synclinorate. The sexine is thin ($1\ \mu$) and finely reticulated, rarely thicker ($2\ \mu$) and coarsely reticulated (in *O. lancifolia*), and the nexine is $\frac{1}{2}$ to $\frac{2}{3}$ thickness of sexine.

Even though the sample of *Oldenlandia* includes pollen from a number of species they are much alike. The ora are always of the type A but variable in form (Fig. 16a-c). Usually the nexinous thickenings surrounding the ora are readily apparent. An exception to this is the pollen of *O. lancifolia* which has only weak nexinous developments adjacent to the apertures and resembles the pollen of *Kohautia* subg. *Pachystigma*, but pollen of these taxa is readily separable on the basis of size and aperture number. Pollen of *Oldenlandia* is most similar to that of *Amphasma*, *Dibrachionostylus* and *Pentodon* among its African allies.

A distinct difference in pollen size between the short- and long-styled flowers of *O. affinis* was noted by Bremekamp (1952). He found that pollen from short-styled plants measure $29.3\ \mu \times 27$ - $30\ \mu$, whereas that from the long-styled plants was only $26\ \mu \times 24$ - $26\ \mu$. For *O. duemmeri* (short style, $25.3\ \mu \times 21.5\ \mu$; long style, $24.0\ \mu \times 21.2\ \mu$) and *O. scopulorum* (short style, $27.3\ \mu \times 24.0\ \mu$; long style, $26.7\ \mu \times 22.0\ \mu$) similar differences have been found in which the pollen from short-styled plants is slightly larger than pollen from long-styled ones. Pollen from short-styled diploid plants of *O. monanthos* average $26.6\ \mu \times 22.0\ \mu$, while pollen from a short-styled octoploid individual is $32.0\ \mu \times 26.7\ \mu$, giving an anticipated larger size for pollen from a polyploid individual than from diploid plants. Both chromosomal and floral differences are also found in *O. herbacea* and pollen available from these plants has the following characteristics: (1) var. *herbacea*, $2x$, homostylous— $25.1\ \mu \times 24.6\ \mu$, sexine thin ($1.7\ \mu$), finely reticulated, apertures 2 (40%) or 3; (2) var. *holstii*, $4x$, short style— $30.6\ \mu \times 30.5\ \mu$, sexine as preceding apertures 3 (85%) or 4; (3) var. *holstii*, $4x$, long style— $29.4\ \mu \times 28.4\ \mu$, sexine and apertures as preceding. These results show that not only is the pollen smaller for the diploid plants than for the tetraploid ones, but that the sexine is thinner, more finely reticulated, and with fewer apertures per grain. Similar differences between the pollen of diploid and tetraploid individuals have also been found for *O. corymbosa* (Lewis, 1964), but for this species both chromosomal races are homostylous. However, in *O. herbacea* the tetraploid variety has both long-styled and short-styled forms. The pollen from $4x$ plants of both floral forms is similar except that the pollen from short-styled plants is slightly larger. Many additional African species not studied from this aspect are heterostylous, but the differences may be similar to those already noted in this study and previously reported by Bremekamp (1963) in the tribe *Psychotrieae*. The results clearly show, however, that a mean-

ingful comparison of pollen size and style type without a prior knowledge of the chromosome number of a taxon is difficult.

PENTODON Hochst.

The most obvious character distinguishing *Pentodon* from *Oldenlandia* is the pentamerous flower of *Pentodon*, while the shape of the placenta, the rather thin and flexible capsule wall, the absence of slime formation when seeds are moistened, and the curious swellings of the testa wall are all very difficult criteria of distinction to use with ease. The genus has two African species with *P. laurentioides* Chiov. rare in Somalia and *P. pentandrus* widespread and considered conspecific by Bremekamp (1952) with the American *P. halei* (T. & G.) Gray.

The common *P. pentandrus* is diploid ($n = 9$) and is similar to *P. halei* (Lewis, 1962b). The bivalents illustrated in Fig. 10 are similar in size and number to those of *Oldenlandia herbacea* (Fig. 8) and to other species of *Oldenlandia* not illustrated. The pollen of *P. pentandrus* is small ($22.8 \mu \times 20 \mu$), subspheroidal, and 3-aperturate with long, narrow colpi, and simple type A ora, 3.3μ high, indefinite horizontally. The sexine is thin (1μ) and finely reticulated, the nexine thinner (0.5μ). The pollen approximates that of *P. halei*, *Amphiasma*, *Dibrachionostylus* and most species of *Oldenlandia*.

II. BASIC CHROMOSOME NUMBER $X = 10$.

OTOMERIA Benth.

Verdcourt (1953a) recognized seven species of *Otomeria* and noted close affinities with *Pentas* and *Tapinopentas* and suggested ". . . that all three genera should be united but the result would be heterogeneous as a whole." More recently Hepper (1960) has reduced *Tapinopentas* to synonymy and distributed its species between *Otomeria* and *Pentas*.

The chromosome complements of *O. elatior* ($n = 10$) and *O. guineensis* ($2n = 20$) are based on $x = 10$. Bivalents illustrated for *O. elatior* (Fig. 11) average ca. 6μ in length and are larger than those for all taxa having $x = 9$. This average chromosome length is similar to that of *Pentas* and *Parapentas* and chromosome morphology thus emphasizes the relationship of these genera. In addition, the morphology of the pollen of *O. elatior* is also similar to that of *Pentas* and *Parapentas*.

PARAPENTAS Bremek.

Bremekamp (1952) based *Parapentas* on *Oldenlandia silvatica* K. Sch., which he felt was more closely allied to *Pentas* than to *Oldenlandia*. He recognized three species, which were subsequently revised and added to by Verdcourt (1953b).

The basic chromosome number for *Parapentas* is $x = 10$ (*P. battiscombei*, $2n = 20$; *P. silvatica*, $n = \text{ca. } 10$). The chromosomes are the same size as those

of *Otomeria* and *Pentas*, but larger than *Oldenlandia*, which supports Bremekamp's earlier conclusions. Palynologically these species are similar to those of *Otomeria* and *Pentas*.

PENTAS BENTH.

In his revision of *Pentas*, Verdcourt (1953c) recognized 32 species which he divided into six subgenera.

The basic number of $x = 10$ for *Pentas*, established earlier (cf. Fagerlind, 1937), was recently confirmed by Lewis (1962b). All previous counts were based on cultivated material. Recently I collected eight taxa in Africa which have been examined cytologically (Appendix 1). These results are in agreement with the earlier data. All taxa are diploid ($n = 10$) excepting *P. lanceolata* subsp. *quartiniana* var. *nemorosa* which is tetraploid ($n = 20$).

Because of many "intermediates" in the *P. lanceolata* complex, Verdcourt (1953c) merged all under *P. lanceolata* and recognized many at the infraspecific level. He mentioned that the subsp. *quartiniana* var. *nemorosa* and the var. *leucaster* both merge with *P. lanceolata* s. s. to form intermediates at the edge of their range. On the basis of known chromosome numbers, the var. *lanceolata* and the var. *leucaster* are diploids while the var. *nemorosa* is tetraploid. Providing individuals typical of var. *nemorosa* are consistently $4x$, then the "intermediates" found by Verdcourt should be triploids and probably sterile. Under these circumstances it is difficult to suggest why so many successful hybridizations exist between the varieties involved in these $2x \times 4x$ crosses. On the other hand, the "intermediates" may represent natural variations of populations which overlap in morphology. This may not be true for all varieties of *P. lanceolata*, but at least for the var. *nemorosa* the population is reproductively isolated from the others and, except for occasional truly triploid intermediates that may be formed, the variability for this taxon is probably inherent. Very often tetraploids are more variable than their diploid ancestors and the tetraploid nature of the var. *nemorosa* is further suggested by a number of characters, e.g., "the var. *nemorosa* is similar to var. *oncostipula* [$2x$] but distinct in the field by virtue of its larger flowers" (Verdcourt, 1953c). Provided that future studies from more individuals substantiate the tetraploidy of var. *nemorosa*, then I believe that the taxon should be recognized at the specific level.

With lengths of about 6μ for *P. longiflora* (Fig. 12) and *P. zanzibarica* var. *intermedia* (Fig. 13), the bivalents of *Pentas* resemble those of *Otomeria*. They are consistently larger than are the bivalents of those genera with a basic number of 9. *Pentas* is allied to *Otomeria* and *Parapentas* because of both chromosome size and number, and this confirms the conclusions of Bremekamp (1952) and Verdcourt (1953a, 1953b, 1953c).

The pollen of *Pentas* is small to medium ($24 \mu \times 18.7 \mu$ to $29 \mu \times 25.5 \mu$), 3- (4-5-) aperturate, with long, narrow colpi and type A ora, about 4μ high, synclinorate or occasionally with the oral belt fading mid-way between the colpi, infrequently with short, horizontal ora. The sexine is $1-1.5 \mu$ thick and reticulations are fine or medium. The nexine is $\frac{1}{2}$ to $\frac{2}{3}$ the thickness of the sexine. This

morphology is similar to *Otomeria* and *Parapentas*, particularly in the striking increase in nexine adjacent to the ora.

As already noted for *Agathisanthemum* and *Oldenlandia*, pollen size for short-styled plants may be slightly larger than pollen for long-styled plants. For *P. lanceolata* var. *leucaster* (long style, $22.8 \mu \times 18.7 \mu$; short style, $24.0 \mu \times 20.9 \mu$), *P. lanceolata* var. *oncostipula* (long style, $22.2 \mu \times 20.5 \mu$; short style, $24.8 \mu \times 21.3 \mu$) and *P. pubiflora* (long style, $23.0 \mu \times 20.7 \mu$; short style, $25.3 \mu \times 22.6 \mu$) there are slight increases in pollen size of short-styled flowers over long-styled flowers without other observable differences.

III. BASIC CHROMOSOME NUMBER $X = 11$.

MANOSTACHYA Bremek.

Two species originally described under *Oldenlandia* form the basis of the genus *Manostachya* (Bremekamp, 1952). According to Bremekamp, the genus is isolated by having reduced axillary inflorescences, short stipular sheaths, subglobose capsules with the upper half superior, testa with thick outer walls forming a network of ridges and rather large pollen. He suggested that *Stephanococcus* (based on *Oldenlandia crepinianus* K. Sch.) is its closest ally. Verdcourt (1958) noted that the seed testa with its network of ridges is quite similar to the pitted testa of members of the tribe *Mussaendeae* grouped in a different subfamily.

The chromosome number of *M. staelioides* is $2n = 44$ which is the only African member of the *Hedyotideae* known with a basic complement of $x = 11$. Mitotic chromosomes from untreated cells measure only 1μ or less in length (Fig. 14) and are somewhat smaller than those of *Oldenlandia* and other genera based on $x = 9$, and much smaller than those of *Pentas*, *Parapentas* and *Otomeria*. In size as well as in number the chromosomes of *Manostachya* more closely approximate those of the woody members of the family such as the *Psychotrieae* or even the more distantly related *Mussaendeae*. *Manostachya* does, however, share the chromosomal number but not the size with the North American species of *Hedyotis* subg. *Edrisia* (Lewis, 1962a). This evidence suggests that this group in North America is the end of an ancient phylad based on $x = 11$. Provided this hypothesis is correct, then *Manostachya* may also represent a second taxon in the *Hedyotideae* having the common rubiaceous set of chromosomes which now exists as a relic complement in the tribe. An additional relic in *Manostachya* may be the ridges or pits found on the outer seed wall, a character unique in the *Hedyotideae* but common to a number of woody (and more primitive ?) tribes in the subf. *Cinchonoideae*.

The pollen of *M. staelioides* is medium ($33.3 \mu \times 28 \mu$), and 3-(4-) aperturate, with long, narrow colpi and simple type A ora. The sexine is 1.7μ thick with medium reticulations and the nexine is 1μ thick, but much thicker adjacent to the ora. This morphology resembles that of most members of the *Hedyotideae*. However, the pollen differs in both size and wall structure from *Stephanococcus*, a genus thought to be allied to *Manostachya*, which has small grains and thin, finely reticulated sexines.

IV. BASIC CHROMOSOME NUMBER UNKNOWN.

It has been impossible to obtain countable cytological material for many known genera of African *Hedyotideae* although pollen from all but two of these has been examined. Most genera not examined cytologically are monotypic with limited distributions and even herbarium material for use in pollen studies is very scarce.

The most important diagnostic features of the pollen for 16 genera are listed in Table 2. Pollen of *Batopedina*, *Carphalea*, *Dirichletia*, *Dolichometra*, *Diotocranus*, *Hedythyrus*, *Pseudonesohedyotis*, *Placopoda*, *Sacosperma*, *Schismatoclada*, *Stephanococcus* and *Thecorchus* is essentially similar in aperture morphology: all are 3- or infrequently 4-colporate with long, narrow colpi and simple, type A ora, as already outlined for the majority of members of the tribe. Ora may be synclinorate (A_1) as for *Hedythyrus*, *Pseudonesohedyotis* and *Sacosperma*, horizontally indefinite (A_2) as for *Dolichometra*, and *Placopoda*, or horizontally distinct (A_3) as for *Batopedina*, *Diotocranus*, *Dirichletia*, *Schismatoclada*, and *Thecorchus*. The ora of *Carphalea* are typically of type A_2 and those of *Stephanococcus* of type A_3 , but for both, synclinorate ora are also found. The sexine is thin (to $1.5\ \mu$) and reticulated, and the grains are small.

Pollen of four genera differ from these. The least different is the very finely reticulated pollen of *Pentanopsis fragrans*, having only slight nexinous thinnings surrounding a type A os. This apparently reduced character is also shared by *Danais* but additionally the os is very narrow and the grains are very small ($16\ \mu \times 14\ \mu$), even though the sexine is coarsely reticulated. Somewhat more isolated are the grains of *Nesohedyotis*, which are quite unlike those of supposedly related species of *Hedyotis* from Asia. They are very small ($11\ \mu \times 14.6\ \mu$), prolate, with a nexine equal in thickness to the sexine and with apertures having long, broad colpi, and compound ora which possess a faint type A os and a large type B os ($3\ \mu$) surrounded by a fine margin. Palynological characters clearly support the elevation of *Hedyotis arborea* to generic rank as *Nesohedyotis arborea* (Bremekamp, 1952). Likewise the pollen of *Hekistocarpa* is prolate in shape, small in size with long, broad colpi. The apertures differ from those of *Nesohedyotis* by the presence of very large (to $8\ \mu$), emarginate ora of type B with no type A os. This aperture type is unique in the *Hedyotideae*.

DISCUSSION

Based on known chromosome complements, the African members of the tribe *Hedyotideae* are separable by number and size into three groups. The largest group of genera is based on $x = 9$ and has small chromosomes ($1.1-2.5\ \mu$), another group is based on $x = 10$ and has medium chromosomes ($3\ \mu >$) and the third group is based on $x = 11$ and has very small chromosomes ($1\ \mu <$). The last is represented in Africa solely by *Manostachya*, even though the complement of $x = 11$ is by far the most common one in this predominantly woody family. However, it is infrequent in the tribe *Hedyotideae* and I suggest that this complement is a relic. The basic complement of $x = 10$ is known for three closely allied genera, *Otomeria*, *Parapentas* and *Pentas*. They are extant genera of probably an old phylad which

Table 2. Summary of the pollen morphology for 16 African genera of *Hedyotideae* lacking known chromosome numbers.

Genus ^a	Pollen size ^b	Aperture number	Os type ^c	Colpus width ^{d, e}	Sexine ^f	Reticulation ^g	Shape
<i>Batopedina</i>	small-med.	3	A ₃	narrow	thin	medium	subspheroidal
<i>Carphalea</i>	medium	3	A ₂ (A ₁)	narrow	medium	medium-coarse	subspheroidal
<i>Danaia</i>	small	3	A ₂	narrow	thin	coarse	subspheroidal
<i>Diotocranus</i>	medium	3	A ₃	narrow	thin	fine	subspheroidal
<i>Dirichletia</i>	medium	4	A ₃	narrow	thin	fine	subspheroidal
<i>Dolichometra</i>	medium	3	A ₂	narrow-medium	thin	medium	subspheroidal
<i>Hedythyrus</i>	small	3	A ₁	narrow	thin	medium-fine	subspheroidal
<i>Hekistocarpa</i>	small	3	B	broad	thin	fine	prolate
<i>Nesohedyotis</i>	small	3	(A ₂) + B	broad	thin-medium	medium	prolate
<i>Pentanopsis</i>	medium	4	A ₂	narrow	thin	very fine	subspheroidal
<i>Placopoda</i>	small	3	A ₂	narrow	thin	medium	subspheroidal
<i>Pseudonesohedyotis</i>	small-med.	3	A ₁	narrow	thin	fine	subspheroidal
<i>Sacosperma</i>	small	3	A ₁	narrow	thin	medium	subspheroidal
<i>Schismatoclada</i> ^h	small	3-4	A ₃	narrow	thin	medium	subspheroidal
<i>Stephanococcus</i>	small	3	A ₃ (A ₁)	narrow	thin-medium	fine-coarse	subspheroidal
<i>Thecorchus</i>	small-med.	3	A ₃	narrow	thin	fine	subspheroidal

^a See Appendix 2 for species studied.
^b Small 10-25 μ, medium 25-50 μ (Erdtman, 1952).
^c See text for explanation of oral types.
^d Narrow to 4 μ, broad > 4 μ.
^e All colpi are long excepting medium in length for *Dolichometra*.
^f Thin to 1.5 μ, medium 1.6-2.9 μ, course 3.0 μ >.
^g Very fine or almost smooth, fine with delicate lumina and muri, medium with lumina ca. 2 μ, coarse with lumina ca. 3 μ.
^h Pollen from short-styled flowers of *S. psychotrioides* mostly 4-aperturate with sexine medium in thickness and coarsely reticulated; from long-styled flowers mostly 3-aperturate with thin sexine finely reticulated.

originated by chromosomal loss from a prototype having $x = 11$. The most common basic number of $x = 9$ is shared by *Agathisanthemum*, *Amphiasma*, *Conostomium*, *Dibrachionostylus*, *Kohautia*, *Oldenlandia*, *Lelya* and *Pentodon*, and the complement probably arose by further reduction in chromosome number from $x = 10$ to $x = 9$. Based on diversity, frequency and geographical distribution of genera, this is the most successful phylad in the *Hedyotideae*.

It is quite possible that the mutations necessary to form each of these hypoeuploid lines occurred more than once, perhaps in Africa, but certainly elsewhere. In North America, *Hedyotis* subg. *Edrisia* is even more marked by chromosomal reduction than its African allies, i.e., $x = 11, 10, 9, 8, 7, 6$ (Lewis, 1962a), yet there is no evidence to suggest other than in situ chromosomal evolution in the subgenus. This would stress a parallel reduction in chromosome number between members of the tribe in these continents, probably at different times and at different rates, which further suggests an inherent mutable tendency for chromosomal reduction. For other areas and for these and other genera, the information is fragmentary, but the basic complement of nine chromosomes is almost universal, viz., *Arcytophyllum* (South America), *Dentella* (Asia), *Bouvardia* (Central and North America), *Hedyotis* and/or *Oldenlandia* (Asia and Australia), and *Manettia* (Central America). The overall propensity in the *Hedyotideae*, therefore, has been one of stabilization of the basic chromosome number of nine, most likely one of reduction from $x = 11$. By having characteristically two pairs of chromosomes less than the chromosomal "epicenter" of the family at $x = 11$, this largely herbaceous tribe is regarded as chromosomally advanced.

The generalized morphology of the pollen for 28 African genera in the *Hedyotideae* is small- to medium-sized, subspheroidal, infrequently prolate; 3-aperturate, with long and narrow colpi having smooth membranes, and with simple type A ora which may be synclinorate, horizontally indefinite, or distinct in outline; sexine 1-2 μ in thickness, simplibaculate, O-L pattern, with fine to coarse lumina and muri giving variously textured reticulations; nexine $\frac{1}{2}$ to $\frac{2}{3}$ thickness of sexine, rarely equal in thickness, but equatorially much thickened adjacent to the colpi and ora.

This pollen description is characteristic of the taxa examined from the two chromosomally-older groups ($x = 11$ and 10), and widespread among taxa of the $x = 9$ phylad. More complex pollen forms are found only among species of the last group. The typical morphology is probably a basic, primitive condition in the tribe, a conclusion supported by the results of the American species of *Hedyotis* (Lewis, 1965). The larger question of how this pollen morphology relates to the general condition for other tribes in the *Rubiaceae* remains unknown. Is it, for instance, indicative of a specialized and "advanced" level already suggested by the chromosome complement? Will a less specialized morphology be found among members of those tribes known to have the basic chromosome number of $x = 11$? Until a palynological survey is undertaken for the *Rubiaceae* such questions must remain unanswered.

Pollen of some species in the tribe differs strikingly from that of the typical, however, and although such pollen has been described for comparatively fewer

genera, the morphology can be of value in problems relating to intergeneric limits and to phylogenetic studies as a whole. The major variations are summarized under eight criteria: the general pollen form is given first and this is followed (after a dash) by the specialized and/or reduced expression, together with representative taxa.

(1) APERTURE NUMBER: 3-aperturate—4-aperturate in some species of all large genera, in *Dirichletia* and *Pentanopsis*; 5- and infrequently 6- to 8-aperturate in *Kohautia* subg. *Pachystigma*; 2-aperturate is very rare and only known for some pollen of *Oldenlandia herbacea*. A trend to greater frequency of apertures was reported for the pollen of the "advanced" species *Hedyotis rosea* Raf. (Lewis, 1965) and also as an advanced trend for some species of *Dicentra* (Stern, 1962).

(2) APERTURE STRUCTURE, THE COLPUS: long colpus—medium lengths in *Conostomium* subg. *Beckia*; short lengths in *C.* subg. *Conostomium* and subg. *Hockstetteria*.

(3a) APERTURE STRUCTURE, THE OS: simple os, type A, followed by complexity and subsequent reduction—addition of crassimarginate os, type B, in *Agathisanthemum*, *Lelya* and as reported for *Hedyotis* subg. *Edrisia* (Lewis, 1965); compound os (types A and B) in which the type A os is barely discernible, in *Nesohedyotis* and some species of *Kohautia* subg. *Kohautia*; disappearance of the type A os, leaving only the type B os in other species of *Kohautia* subg. *Kohautia*. This last kind of os was reported for some species of *Hedyotis* subg. *Edrisia* which are thought to represent the most advanced, but highly reduced, elements of that subgenus (Lewis, 1965).

(3b) APERTURE STRUCTURE, THE OS: simple os, type A, followed by reduction—equatorial extensions of the os reduced and barely discernible in *Danais*, *Kohautia* subg. *Pachystigma*, *Oldenlandia herbacea* and *Pentanopsis*.

(4) POLLEN SIZE: medium-small (ca. 20-30 μ)—very small grains in *Danais*, *Kohautia* subg. *Kohautia* and *Nesohedyotis*, a trend already noted for the pollen of *Hedyotis rosea* (Lewis, 1965).

(5) POLLEN SHAPE: subspheroidal—oblate in *Hekistocarpa* and *Nesohedyotis*.

(6) SUPRATEGILLAR ELEMENTS: none—with verrucae in *Conostomium* subg. *Conostomium*. Stern (1962) noted that the advanced *Dicentra* subg. *Dactylicapnos* has pollen with verrucate sexines, while the more primitive subgenera have reticulate, foveolate or rugulate sexines.

(7) SEXINE RETICULATION: medium or fine—very fine reticulation (appearing $\pm$ smooth) in *Pentanopsis*; coarse reticulation in *Danais*, *Kohautia* subg. *Pachystigma*, and *Oldenlandia herbacea*. Pollen having coarse reticulations also typifies the most advanced species of *Hedyotis* subg. *Edrisia* (Lewis, 1965).

(8) SEXINE THICKNESS: medium-fine in thickness (1-2 μ)—thick sexine with associated coarse baculae in *Conostomium* subg. *Conostomium*, *C.* subg. *Hockstetteria*, *Kohautia* subg. *Kohautia* and *Lelya*. Thicker sexines were also reported among the most advanced species in *Hedyotis* subg. *Edrisia* (Lewis, 1965).

Other modifications in pollen which might be added include the extremely large os (type B) with a reduced margin in *Hekistocarpa*. Pollen of this genus also

has very broad colpi as does pollen from *Nesohedyotis*. These expressions are most exceptional among members of the *Hedyotideae* and require additional study and confirmation.

It is obvious that the majority of these modifications characterize only a few taxa. If a value of "0" represents the typical expression for each of the pollen characters noted above, "1" represents the atypical expression for each, and values of "2" and "3" for additional alternatives of aperture number and oral structure, then the taxa can be ranked according to their divergence from the typical pollen form. Summarizing for the *Hedyotideae* of Africa, where "0" represents the typical pollen morphology, 28 genera with the number of species examined given in parenthesis rank as follows:

"0-0.6"—*Amphasma* (2), *Batopedina* (1), *Carphalea* (2), *Dibrachionostylus* (1), *Diotocranus* (1), *Dirichletia* (1), *Dolichometra* (1), *Hedythyrsus* (1), *Manostachya* (1), *Oldenlandia* (13), *Otomeria* (1), *Parapentas* (2), *Pentas* (3), *Pentodon* (1), *Placopoda* (1), *Pseudonesohedyotis* (1), *Sacosperma* (1), *Schismatoclada* (2), *Stephanococcus* (1), *Theocorchus* (1).

"1.3-1.5"—*Agathisanthemum* (3), *Lelya* (1).

"2.7-3.0"—*Conostomium* (4), *Danais* (2), *Pentanopsis* (1).

"4.0" —*Hekistocarpa* (1), *Kohautia* (20), *Nesohedyotis* (1).

The genera most removed palynologically from the generalized morphology are, therefore, *Conostomium*, *Danais*, *Hekistocarpa*, *Kohautia*, *Nesohedyotis* and *Pentanopsis*, with *Agathisanthemum* and *Lelya* less strikingly so.

It is also relevant to know whether or not these genera exhibiting specialized and/or reduced expressions for pollen are characterized by unique sporophytic expressions. By and large the African representatives of the tribe are herbs with bisexual, homostylous or heterostylous flowers having small or medium corollas and with many, wingless seeds in readily dehiscent capsules. Departures from this morphology are found for *Kohautia* (short-styled flowers only), *Conostomium* (typically long-styled flowers only and greatly enlarged corollas), *Lelya* (tardily dehiscent, nut-like capsules with few seeds), *Nesohedyotis* (small trees with unisexual flowers), *Pentanopsis* (shrubs with large corollas), *Danais* (winged seeds [transferred from the tribe *Cinchoneae* and considered rather isolated by Bremekamp, 1952]) and *Hekistocarpa* (shrub).

Hence there is a marked correlation between genera illustrating atypical male gametophytic characters on the one hand with those having atypical sporophytic characters on the other. A similar correlation, often involving the same features for plants of both generations, was also observed for the North American members of the tribe (Lewis, 1965).

The value of palynological and chromosomal data as an aid to classification has been demonstrated for the North American members of the *Hedyotideae* (Lewis, 1962a, 1965). In Africa the unique chromosome complement of $x = 11$ for *Manostachya* supports the isolated position of this genus in relation to *Oldenlandia*

(Bremekamp, 1952). The chromosome complement of $x = 10$ also supports a position for *Parapentas* in the immediate vicinity of *Otomeria* and *Pentas* rather than with *Oldenlandia* as concluded by Bremekamp (1952).

Agathisanthemum, *Conostomium*, *Kohautia*, *Lelya* and *Nesohedyotis* each possesses a pollen morphology different from all known species of *Oldenlandia* and *Hedyotis* in Afro-Asia. These palynologically distinct genera should not be included in *Oldenlandia* or *Hedyotis*, as they have been until Bremekamp's (1952) recent revision. Palynological data also support the generic rank for *Pentanopsis*, a genus which should be considered part of the oldenlandiaceous group allied to *Kohautia*. Two genera, *Danais* and *Hekistocarpa*, never closely associated with *Oldenlandia*, possess a number of pollen characteristics unknown to *Oldenlandia* and its immediate allies, and palynologically these genera are not closely associated with the epicenter of the tribe. Finally, the pollen morphology of *Schismatoclada* supports its transfer from the *Cinchoneae* to the *Hedyotideae* (Verdcourt, 1958).

No variation in pollen and chromosomal morphology parallels the gross morphology characteristics used in separating *Amphiasma*, *Dibrachionostylus* and *Pentodon* from *Oldenlandia*. Obviously the absence of cytopalynological characteristics does not automatically relegate these genera to subdivisions of *Oldenlandia*. The similarity does indeed suggest that too much emphasis might have been placed on certain exo- and endomorphic criteria of only secondary value in delimiting genera. A re-evaluation in these instances is required. The genus *Amphiasma* is distinguished from *Oldenlandia* only by its dorsiventrally flattened seeds and tubular stipules, yet the latter character is weakened by the reduced stipular sheath known for *A. divaricantum* (Engl.) Bremek. The shape of the seed is in itself a minor difference on which to base genera, particularly when this is not accompanied by alterations in the testal cells or by craters, hilar ridges or others. In my opinion *Amphiasma* would be better accommodated as a subgroup of *Oldenlandia*. The same judgment applies to *Dibrachionostylus*: loculicidally and septicidally dehiscent capsules of *Oldenlandia* are insufficient evidence for generic separation. This monotypic genus should be replaced in *Oldenlandia*.

Apart from having pentamerous flowers and swellings on the lateral testal walls, the remaining criteria (p. 194) separating *Pentodon* from *Oldenlandia* are of secondary value. Moreover the unusual testal swellings known for *P. pentandrus* and *P. halei* are not found to the same extent for *P. laurentioides* Chiov. and their near absence in this species clearly decreases the generic importance of this specialization. Perhaps the closest allies of *Pentodon*, however, are Asian and Oceanic in origin, and until these can be studied in detail, the genus should be retained.

The differences in pollen and/or sporophytic morphology of some additional genera (e.g., *Eionitis*) are not significant enough to separate them from *Oldenlandia* and this suggests that an even more conservative treatment for members of the tribe *Hedyotideae* in Africa is in order when more material is available for cytological and comparative morphological studies. Additional research, particularly of Asian taxa, is necessary before far-reaching changes in classification can be made.

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APPENDIX 1

Procedures, Materials and Results of Chromosomal Study

Immature flower buds were fixed in 4 parts chloroform, 3 parts absolute ethanol and 1 part glacial acetic acid, and airmailed from Africa to England for storage at -40°C. From one to seven months following fixation, whole buds were squashed in 2% acetic-orcein and those preparations showing pollen mother cell meiosis were mounted in euparal for permanent reference.

To supplement the chromosome counts obtained from field collections, seeds obtained directly from Africa or from herbarium specimens were sown at the Royal Botanic Gardens, Kew. At maturity the apical meristems or whole buds from these plants were treated as above for both mitotic and meiotic counts. Seeds from some species remained viable on herbarium sheets for periods up to five years.

Voucher specimens for my collections, including those from natural and greenhouse conditions, are deposited at the Missouri Botanical Garden (MO) and, with

a few exceptions, at the Royal Botanic Gardens (K) and the U. S. National Museum (US). For each successful count, the original locality of the collection, the collector and number and the locality of the herbarium voucher, if other than the author's, are given below under the appropriate taxa. Following these data the number of plants examined for each count is given in parentheses together with a notation of the seed source when applicable. The genera and subgenera are arranged alphabetically.

Taxon	<i>n</i>	<i>2n</i>	Locality and voucher
AGATHISANTHEMUM			
<i>A. bojeri</i> Klotzsch subsp. <i>bojeri</i>	9	18	TANGANYIKA: Tanga Region, Tanga Area, 5.2 miles N. of Tanga, <i>Lewis</i> 6056 (1); 16 miles W. of Tanga, <i>Lewis</i> 6063 (1).
<i>A. bojeri</i> subsp. <i>australe</i> Bremek.	—	18	S. AFRICA: Natal, Hlabisa Dist., Charters Creek, <i>Lewis</i> 6299 (2).
<i>A. globosum</i> (Hochst. ex A. Rich.) Klotzsch ex Bremek.	—	36	KENYA: Rift Valley Prov., West Suk Dist., 0.3 miles N. of Keringet, <i>Lewis</i> 5987 (1). N. RHODESIA: N. W. Prov., Mwinilunga Dist., Zambesi River rapids, 4 miles N. of Kalene mission, <i>Lewis</i> 6209 (1).
AMPHIASMA			
<i>A. merenskyanum</i> Bremek.	—	18	S. W. AFRICA: Kaokoveld Dist., 6 miles N. of Kamanjob, <i>De Winter & Leistner</i> 5103 (K) (1 ¹).
<i>A. sp.</i>	—	ca.36	S. W. AFRICA: Walvis Bay Dist. E. edge of Namid Desert, <i>Lewis</i> 6396 (1 ²).
CONOSTOMIUM subg. BECKIA			
<i>C. kenyense</i> Bremek.	—	ca.36	KENYA: S. Prov., Machakos Dist., 44 miles from Thika, Yatta, <i>Archer</i> 88 (K) (1 ¹).
CONOSTOMIUM subg. HOCHSTETTERIA			
<i>C. natalense</i> (Hochst.) Bremek.	9	18	S. AFRICA: Cape, Bizana Dist., 16 miles W. of Bizana, <i>Lewis</i> 6370 (2 ²); Transvaal, Barberton Dist., 25.8 miles S. E. of Barberton, <i>Lewis</i> 6332 (1). SWAZILAND: Mbabane, Ukutula, <i>Lewis</i> 6321 (3).
DIBRACHIONOSTYLUS			
<i>D. kaessneri</i> (S. Moore) Bremek.	9	—	KENYA: Central Prov., Nairobi National Park, <i>Lewis</i> 5904 (2).
KOHAUTIA subg. KOHAUTIA			
<i>K. aspera</i> (Heyne ex Roth) Bremek.	18	36	ETHIOPIA: Harar Prov., N. E. edge of Lake Alemaya, <i>Lewis</i> 5874 (4).
<i>K. caespitosa</i> Schnizl. var. <i>caespitosa</i>	—	36	S. AFRICA: Natal, Hlabisa Dist., 14 miles N. W. of Hluhluwe, <i>Lewis</i> 6311 (1).
<i>K. caespitosa</i> var. <i>ameniensis</i> (K. Krause) Bremek.	—	36	TANGANYIKA: Tanga Region, Lushoto Area, Mombo-Lushoto Rd., <i>Samsei</i> 3070 (K) (1 ¹).
<i>K. coccinea</i> Royle var. <i>coccinea</i>	9	18	ETHIOPIA: Harar Prov., Collubi, <i>Lewis</i> 5900 (2).
<i>K. coccinea</i> var. <i>macrodonta</i> (Bak.) Bremek.	—	18	KENYA: Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, <i>Lewis</i> 5952 (2).

Taxon	<i>n</i>	<i>2n</i>	Locality and voucher
<i>K. cynanchica</i> DC.	9	18	SWAZILAND: 2.5 miles N. of Golela, <i>Lewis</i> 6313 (3).
<i>K. grandiflora</i> DC.	9	—	UGANDA: N. Prov., Karamoja Dist., 4 miles N. E. of Irire, <i>Lewis</i> 5997 (3); 7 miles W. of Namalu prison, base of Mt. Oboa, <i>Lewis</i> 5990 (1).
KOHAUTIA subg. PACHYSTIGMA			
<i>K. longifolia</i> Klotzsch var. <i>longifolia</i> —	—	36	N. RHODESIA: N. Prov., Abercorn Dist., Sunzu Gorge, <i>Lewis</i> 6094 (3 ¹).
<i>K. virgata</i> (Willd.) Bremek.	27	54	S. AFRICA: Natal, Hlabisa Dist., Charters Creek, <i>Lewis</i> 6294 (2); Transvaal, Pretoria Dist., Pretoria, Wonderboom, <i>Lewis</i> 6348 (1); Transvaal, W. of Pretoria, <i>Lewis</i> 6356 (1 ²). S. RHODESIA: Nuanetsi Dist., Nuanetsi River, <i>Drummond & Rutherford-Smith</i> 7554 (SRGH) (2 ¹).
LELYA			
<i>I. prostrata</i> (R. Good) W. H. Lewis var. <i>prostrata</i>	18	—	TANGANYIKA: S. Highlands Region, Iringa Area, 4.5 miles N. E. of John's Corner, <i>Lewis</i> 6067 (2).
MANOSTACHYA			
<i>M. staelioides</i> (K. Sch.) Bremek.	—	44	N. RHODESIA: N. W. Prov., Solwezi Dist., 1 mile S. E. of Solwezi, <i>Lewis</i> 6128 (2).
OLDENLANDIA subg. ANEURUM			
<i>O. lancifolia</i> (Schumach.) DC. var. <i>lancifolia</i>	18	—	CAMEROUN: 36 km. N. E. of Douala, <i>Lewis</i> 6407 (1 ²). KENYA: Central Prov., Embu Dist., Embu, <i>Lewis</i> 5905 (1).
<i>O. lancifolia</i> var. <i>scabridula</i> Bremek.	18	—	N. RHODESIA: N. W. Prov., Mwinilunga Dist., Mujileshi River, 5-6 miles S. E. of Angola—N. R. border, <i>Lewis</i> 6167 (1).
OLDENLANDIA subg. ANOTIDOPSIS			
<i>O. angolensis</i> K. Sch.	9	—	N. RHODESIA: N. Prov., Abercorn Dist., Chila Lake, Abercorn, <i>Lewis</i> 6123 (1).
	18	—	N. RHODESIA: N. W. Prov., Mwinilunga Dist., Zambesi River, 4 miles N. of Kalene mission, <i>Lewis</i> 6201 (2).
<i>O. cephalotes</i> (Hochst.) O. Ktze.	9	—	SWAZILAND: Mbabane, Mbabane River, <i>Lewis</i> 6314 (1).
	—	36	SWAZILAND: Komati River by Forbes Reef-Piggs Peak Rd., <i>Lewis</i> 6331 (1).
<i>O. goreensis</i> (DC.) Summerhayes	18	36	ANGOLA: Moxico Dist., 2 miles W. of Jimbe River by Caianda-Mwinilunga Rd., <i>Lewis</i> 6213 (1). KENYA: Rift Valley Prov., Trans Nzoia Dist., Kitale, <i>Lewis</i> 5980 (2). N. RHODESIA: N. Prov., Abercorn Dist., 5.5 miles S. W. of Abercorn, <i>Lewis</i> 6120 (1); N. W. Prov., Mwinilunga Dist., 1-4 miles E. of Angola-N. R. border, <i>Lewis</i> 6132 (1). TANGANYIKA: W. Region, Kigoma Area, Kasoji, <i>Newbould & Harley</i> 4419 (1 ¹). UGANDA: Buganda Prov., Mengo Dist., 3.5 miles N. E. of Kampala, <i>Lewis</i> 6022 (1).

Taxon	<i>n</i>	<i>2n</i>	Locality and voucher
OLDENLANDIA subg. CEPHALANTHIUM			
<i>O. scopulorum</i> Bullock var. <i>scopulorum</i>	9	—	KENYA: Rift Valley Prov., Laikipia Dist., 3 miles W. of Thomson's Falls, <i>Lewis</i> 6950 (1).
<i>O. scopulorum</i> var. <i>lanceolata</i> Bremek.	9	—	KENYA: Rift Valley Prov., Naivasha Dist., Lake Naivasha, <i>Lewis</i> 5949 (2).
OLDENLANDIA subg. HEMICEPHALUM			
<i>O. saxifragoides</i> Chiov.	—	18	SOMALIA: Eil, <i>Hemming</i> 1673 (K) (2 ¹).
OLDENLANDIA subg. HYMENOPHYLLUM			
<i>O. echinulosa</i> K. Sch.	9	18	TANGANYIKA: S. Highlands Region, Rungwe Area, S. slopes of Poroto Mts., <i>Lewis</i> 6091 (2).
<i>O. pellucida</i> Hiern	—	18	TANGANYIKA: W. Region, Mpanda Area, Belengi, 12 miles N. of Kasogi, <i>Harley</i> 9137 (K) (2 ¹).
OLDENLANDIA subg. OCTONEURUM			
<i>O. affinis</i> (Roem. & Schult.) DC.	—	18	CONGO (BRAZZA.): Diosso, <i>Lewis</i> 6402 (2 ²). GHANA: E. Region, Accra Dist., Legon, <i>Lewis</i> 6419 (1 ²). NIGERIA: W. Region, Benin Prov., Iyokuselu Dist., W.A.I.F.O.R., <i>Daramola</i> s. n. (FHI) (2 ¹). S. AFRICA: Natal, Port Shepstone Dist., nr. Port Edward, <i>Lewis</i> 6366 (2 ²); Natal, Hlabisa Dist., Charters Creek, <i>Lewis</i> 6298 (2). INDIA: Hyderabad, Warangal, <i>Lewis</i> 6375 (1 ²).
OLDENLANDIA subg. OLDENLANDIA			
<i>O. capensis</i> L. f. var. <i>capensis</i>	9	18	ANGOLA: Moxico Dist., 2 miles W. of Jimbe River by Caianda-Mwinilunga Rd., <i>Lewis</i> 6214 (2). N. RHODESIA: N. W. Prov., Mwinilunga Dist., Mujileshi River, 5-6 miles S. E. of Angola-N. R. border, <i>Lewis</i> 6173 (1). TANGANYIKA: Tanga Region, Tanga Area, 4 miles N. of Tanga, <i>Lewis</i> 6059 (1).
	—	36	N. RHODESIA: S. Prov., Livingstone Dist., Livingstone I., Victoria Falls, <i>Lewis</i> 6249 (2).
<i>O. capensis</i> var. <i>pleiosepala</i> Bremek.	9	18	N. RHODESIA: N. W. Prov., Mwinilunga Dist., 4 miles N. of Kalene mission, <i>Lewis</i> 6210 (2).
	9, 18	—	N. RHODESIA: N. W. Prov., Mwinilunga Dist., West Lunga River nr. Mwinilunga, <i>Lewis</i> 6131 (2, 2x; 1, 4x).
<i>O. corymbosa</i> L. var. <i>corymbosa</i>	9	18	Based on 7 collections from CAMEROUN, DAHOMEY, GABON, NIGERIA, TOGO, BRAZIL (cf. <i>Lewis</i> , 1964).
	18	36	Based on 13 collections from ETHIOPIA, KENYA, NIGERIA, INDIA (cf. <i>Lewis</i> , 1964).
	27	54	Based on 1 collection from TOGO (cf. <i>Lewis</i> , 1964).

Taxon	<i>n</i>	<i>2n</i>	Locality and voucher
<i>O. corymbosa</i> var. <i>subpedunculata</i> O. Ktze.	18	35	Based on 6 collections from KENYA, s. RHODESIA, TANGANYIKA (cf. Lewis, 1964).
<i>O. fastigiata</i> Bremek.	—	18	TANGANYIKA: Tanga Region, Handeni Area, 9 miles S. W. of Handeni, <i>Lewis</i> 6064 (2 ¹).
<i>O. herbacea</i> (L.) Roxb. var. <i>herbacea</i>	9	18	KENYA: Central Prov., Nairobi National Park, <i>Lewis</i> 5905 (1). N. RHODESIA: N. Prov., Abercorn Dist., 2 miles S. W. of Abercorn, <i>Lewis</i> 6122 (1); N. W. Prov., Mwinilunga Dist., 1 mile E. of Ikelengi, <i>Lewis</i> 6190 (1); Zambesi River, 4 miles N. of Kalene mission, <i>Lewis</i> 6202 (1). s. RHODESIA: Salisbury Dist., Salisbury, Cranborne, <i>Lewis</i> 6251 (2). UGANDA: Buganda Prov., Entebbe Dist., 4 miles N. E. of Entebbe, <i>Lewis</i> 6017 (2). SWAZILAND: Komati River by Forbes Reef-Piggs Peak Rd., <i>Lewis</i> 6328 (1); Mbabane, Mbabane River, <i>Lewis</i> 6315 (1).
<i>O. herbacea</i> var. <i>flaccida</i> Bremek.	9	—	ETHIOPIA: Harar Prov., 1.8 km. W. of Errer River by Harar-Giggiga Rd., <i>Lewis</i> 5861 (2). CONGO(LÉOP.): Katanga Prov., Lualaba Dist., 13 miles S. S. W. of Mutschatsha, <i>Lewis</i> 6237 (2).
<i>O. herbacea</i> var. <i>goetzei</i> Bremek.	9	18	CONGO(LÉOP.): Katanga Prov., Lualaba Dist., 15 miles N. N. W. of Kalene mission, <i>Lewis</i> 6228 (2); 13 miles S. S. W. of Mutschatsha, <i>Lewis</i> 6238 (2).
<i>O. herbacea</i> var. <i>holstii</i> (K. Sch.) Bremek.	—	36	KENYA: Coast Prov., Taita Dist., S. E. slope of Mt. Vuria, <i>Lewis</i> 5931 (3).
<i>O. linearis</i> DC.	9	18	KENYA: Rift Valley Prov., Trans Nzoia Dist., Kitale, <i>Lewis</i> 5979 (2); E. N. E. slope of Mt. Elgon, <i>Lewis</i> 5953 (2), 5977 (1). TANGANYIKA: W. Region, Kigoma Area, Kasoje, <i>Newbould & Harley</i> 4415 (K) (1 ¹). UGANDA: N. Prov., Karamoja Dist., 7 miles W. of Namalu, <i>Lewis</i> 5991 (1).
<i>O. marginata</i> Bremek.	—	36	KENYA: Coast Prov., Lamu Dist., Osina, <i>Greenway & Rawlings</i> 9289 (K) (2 ¹).
<i>O. praetermissa</i> Bremek.	18	36	GHANA: E. Region, Accra, <i>Lewis</i> 6416 (2 ²).
<i>O. cf. pumila</i> (L. f.) DC.	9	18	UGANDA: W. Prov., Toro Dist., Queen Elizabeth National Park, N. W. shore of Lake Edward, <i>Lewis</i> 6009 (3).
<i>O. pumila</i> (L. f.) DC.	—	18	INDIA: Hyderabad, Osmania University campus, <i>Lewis</i> 6376 (2 ²).
<i>O. somala</i> Chiov. ex Bremek.	—	36	TANGANYIKA: Lake Region, Musoma Area, Nata Rest House, <i>Tanner</i> 4121 (K) (3 ¹).
OLDENLANDIA subg. OROPHILUM			
<i>O. johnstonii</i> (Oliv.) K. Sch.	—	18	KENYA: Central Prov., Nairobi National Park, <i>Lewis</i> 5906 (1).

Taxon	<i>n</i>	<i>2n</i>	Locality and voucher
<i>O. monanthos</i> (Hochst. ex A. Rich.) Hiern	9	18	ETHIOPIA: Harar Prov., Collubi, <i>Lewis</i> 5899 (2); 3 km. E. of Gara Ades, <i>Lewis</i> 5880 (1).
	27	—	KENYA: Nyanza Prov., Kericho Dist., S. W. Mau Forest, <i>Kerfoot</i> 2781 (K) (1 ¹).
	36	—	KENYA: Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, <i>Lewis</i> 5955 (2).
<i>O. rupicola</i> (Sand.) O. Ktze.	9	18	TANGANYIKA: Tanga Region, Lushoto Area, Herkulu Tea Estate, ca. 7 miles E. of Soni, <i>Lewis</i> 6051 (3).
OLDENLANDIA subg. POLYCARPUM			
<i>O. duemmeri</i> S. Moore	9	—	UGANDA: Buganda Prov., Entebbe Dist., 4 miles N. E. of Entebbe, <i>Lewis</i> 6018 (2).
OLDENLANDIA subg. STACHYANTHUS			
<i>O. flosculosa</i> Hiern	—	36	ZANZIBAR: Cheraka, mile 1b, <i>Faulkner</i> 2536 (K) (2 ¹).
OTOMERIA			
<i>O. elatior</i> (A. Rich. ex DC.) Verdc.	10	—	ANGOLA: Moxico Dist., 2 miles W. of Jimbe River on Caianda-Mwinilunga Rd., <i>Lewis</i> 6215 (3). N. RHODESIA: N. Prov., Abercorn Dist., Sunzu Gorge, <i>Lewis</i> 6097 (1). UGANDA: Buganda Prov., Mengo Dist., 3.5 miles N. E. of Kampala, <i>Lewis</i> 6024 (2).
<i>O. guineensis</i> Benth.	—	20	LIBERIA: Monrovia, <i>Wrigley & Melville</i> 703 (K) (3 ¹).
PARAPENTAS			
<i>P. battiscombei</i> Verdc.	—	20	KENYA: Central Prov., Meru Dist., vicinity of Chogoria, <i>Lewis</i> 5914 (2 ¹).
<i>P. silvatica</i> (K. Sch.) Bremek.	ca. 10	—	TANGANYIKA: Tanga Region, Lushoto Area, ca. 7 miles E. of Soni, <i>Lewis</i> 6049 (1).
PENTAS			
<i>P. lanceolata</i> (Forsk.) Defflers	—	20	S. AFRICA: Natal, Port Shepstone Dist., Mtamvuna River, nr. Port Edward, <i>Lewis</i> 6367 (1 ²).
<i>P. lanceolata</i> subsp. <i>lanceolata</i> var. <i>lanceolata</i>	10	—	KENYA: Rift Valley Prov., Naivasha Dist., 10 miles E. of Naivasha, <i>Lewis</i> 5928 (2).
<i>P. lanceolata</i> subsp. <i>quartiniana</i> (A. Rich.) Verdc. var. <i>leucaster</i> (Krause) Verdc.	10	—	KENYA: Coast Prov., Taita Dist., S. E. face of Mt. Vuria, <i>Lewis</i> 5930 (2); Rift Valley Prov., Trans Nzoia Dist., Kitale, <i>Lewis</i> 5982 (1).
<i>P. lanceolata</i> subsp. <i>quartiniana</i> var. <i>nemorosa</i> (Chiov.) Verdc.	20	—	KENYA: Central Prov., Embu Dist., 2 miles N. E. of Runyenje's, <i>Lewis</i> 5910 (2).
<i>P. lanceolata</i> subsp. <i>quartiniana</i> var. <i>oncostipula</i> (K. Sch.) Verdc.	—	20	TANGANYIKA: Tanga Region, Lushoto Area, ca. 7 miles E. of Soni, <i>Lewis</i> 6040 (1).

Taxon	<i>n</i>	<i>2n</i>	Locality and voucher
<i>P. longiflora</i> Oliv.	10	—	KENYA: Central Prov., Meru Dist., 5 miles S. of Kanyekine, <i>Lewis</i> 5915 (2); Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, <i>Lewis</i> 5956 (1).
<i>P. longiflora</i> f. <i>glabrescens</i> Verdc.	10	—	KENYA: Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, <i>Lewis</i> 5962 (2).
<i>P. pubiflora</i> S. Moore	10	—	KENYA: Rift Valley Prov., Trans Nzoia Dist., E. N. E. slope of Mt. Elgon, <i>Lewis</i> 5963 (2).
<i>P. zanzibarica</i> (Klotzsch) Vatke var. <i>intermedia</i> Verdc.	10	—	UGANDA: W. Prov., Toro Dist., Bunyangabu Co., nr. Nyakalengija, <i>Lewis</i> 6005 (2).
PENTODON			
<i>P. pentandrus</i> (Schum. & Thonn.) Vatke var. <i>pentandrus</i>	9	—	TANGANYIKA: Tanga Region, Tanga Area, 7 miles N. of Tanga, <i>Lewis</i> 6055 (1). UGANDA: Buganda Prov., Mengo Dist., Kampala, King's Lake, <i>Lewis</i> 6027 (1).

¹ Seeds obtained from herbarium specimens; the chromosomal voucher is in most cases the original collection.

² Seeds sent by Mr. S. R. J. White from Africa or Mr. B. Bahadur from India; the chromosomal voucher is from greenhouse-matured seedlings.

APPENDIX 2

Palynological Procedures and Materials

Whole flowers, mature buds, or anthers only were removed from herbarium specimens and acetolyzed according to the procedure outlined by Erdtman (1952). Most collections were also chlorinated before being mounted in glycerin jelly and sealed with paraffin. A complete set of slides is maintained at the Missouri Botanical Garden and duplicates of many are filed with either the Palynological Laboratory, Stockholm-Solna, or the Royal Botanic Gardens, Kew.

Palynological terminology follows Erdtman (1952) and Lewis (1965). Measurements for quantitative characters are based on 10 random samples with the average of these given throughout the descriptions.

Herbarium vouchers of my collection are deposited at the Missouri Botanical Garden (MO), the Royal Botanic Gardens (K) and the U. S. National Museum (US). Collections of others are with these institutions or with the Naturhistoriska Riksmuseum, Stockholm (S) as indicated. The genera and species studied are listed alphabetically below together with the collector and number, herbarium where specimen filed (excepting the author's) and the country of collection.

Agathisanthemum bojeri Klotzsch subsp. *bojeri*, *Lewis* 6056 (Tanganyika). *A. globosum* (Hochst. ex A. Rich.) Klotzsch ex Hiern, *Irwin* 237 (K) (Kenya). *A. quadricostatum* Bremek., *Richards* 1369 (K) (N. Rhodesia).

Amphiasma benguellense (Hiern) Bremek., Grossweiler 9686 (K) (Angola). *A. merenskyanum* Bremek., Dinter 6836 (S) (S. W. Africa).

Batopedina linearifolia (Bremek.) Verdc., Fanshawe 4143 (K) (N. Rhodesia).

Carphalea madagascariensis Lam., Afzelius s. n. (S) (Madagascar). *C. pervilleana* H. Brown, Afzelius s. n. (S) (Madagascar).

Conostomium kenyense Bremek., Adamson B3564 (K) (Kenya). *C. longitubum* (Beck) Cuf., White 175 (K) (Somalia). *C. natalense* (Hochst.) Bremek., Lewis 6321 (Swaziland). *C. quadrangulare* (Rendle) Cuf., Napier 2067 (K) (Kenya).

Danais fragrans Comm. ex Gaertn., Anderson 103 (S) (Mauritius).

Dibrachionostylus kaessneri (S. Moore) Bremek., Lewis 5904 (Kenya).

Diotocranus lebrunii Bremek., Robinson 4548 (K) (N. Rhodesia).

Dirichletia sp., Newbould 3509 (S) (Kenya).

Dolichometra leucantha K. Sch., Drummond & Hemsley 3449 (K) (Tanganyika).

Hedythyrus thamnoideus (K. Sch.) Bremek., Dale 667 (K) (Congo, Léop.).

Hekistocarpa minutiflora Hook. f., Dusén s. n. (S) (Cameroon), FHI 30613 (K) (Nigeria).

Kohautia amatymbica Eckl. & Zeyh., Methuen 131 (K) (S. Rhodesia). *K. angolensis* Bremek., Pearson 2382 (K) (Angola). *K. aspera* (Heyne ex Roth) Bremek., Lewis 5858 (Ethiopia). *K. caespitosa* Schnizl., Lewis 6311 (S. Africa). *K. coccinea* Royle, Lewis 5952 (Kenya). *K. cuspidata* (K. Sch.) Bremek., Wild 4762 (K) (S. Rhodesia). *K. cynanchica* DC., Lewis 6313 (Swaziland). *K. effusa* (Oliv.) Bremek., Anderson 1046 (K) (Kenya). *K. grandiflora* DC., Lewis 5990 (Uganda). *K. lasiocarpa* Klotzsch, Chase 5922 (K) (S. Rhodesia). *K. longifolia* var. *longifolia*, Lewis 6094 (N. Rhodesia). *K. obtusiloba* (Hiern) Bremek., Faulkner 810 (K) (Tanganyika). *K. omahekensis* (K. Krause) Bremek., Lugard 111 (K) (S. Rhodesia). *K. platyphylla* (K. Sch.) Bremek., Reynolds B9244 (K) (Ethiopia). *K. prolixipes* (S. Moore) Bremek., Jex-Blake 16 (K) (Kenya). *K. ramosissima* Bremek., Leistner 2248 (K) (S. Africa). *K. raphidophylla* Bremek., Pearson 4682 (K) (S. Africa). *K. senegalensis* C. & S., Brooks 7 (K) (Gambia). *K. somaliensis* Bremek., Glover & Gilliland 301 (K) (Somalia). *K. virgata* (Willd.) Bremek., Lewis 6294 (S. Africa).

Lelya prostrata (R. Good) W. H. Lewis var. *prostrata*, Lewis 6067 (Tanganyika).

Manostachya staelioides (K. Sch.) Bremek., Lewis 6128 (N. Rhodesia).

Nesohedyotis arborea (Roxb.) Bremek., Kerr 8 (K) (St. Helena).

Oldenlandia capensis L. f., Lewis 6214 (Angola). *O. cephalotes* (Hochst.) O. Ktze., Lewis 6314 (Swaziland). *O. corymbosa* L. var. *corymbosa* and var. *subpedunculata* O. Ktze., (cf. Lewis, 1964). *O. duemmeri* S. Moore, Lewis 6018 (Uganda). *O. echinulosa* K. Sch., Lewis 6091 (Tanganyika). *O. goreënsis* (DC.) Summerhayes, Lewis 6120 (N. Rhodesia). *O. herbacea* (L.) Roxb. var. *herbacea*, Lewis 6251 (S. Rhodesia); var. *holstii* (K. Sch.) Bremek., Lewis 5931 (Kenya). *O. johnstonii* (Oliv.) K. Sch., Lewis 5906 (Kenya). *O. lancifolia* (Schumach.) DC. var. *scabridula* Bremek., Lewis 6023 (Uganda). *O. linearis* DC., Lewis 5979 (Kenya). *O. monanthos* (Hochst. ex A. Rich.) Hiern, Lewis 5899 (Ethiopia), Lewis 5955 (Kenya). *O. praetermissa* Bremek., Lewis 6416 (Ghana). *O. rupicola* (Sond.) O. Ktze., Lewis 6051 (Tanganyika). *O. scopulorum* Bullock, Lewis 5949 (Kenya).

Otomeria elatior (A. Rich. ex DC.) Verdc., Lewis 6024 (Uganda).

Parapentas battiscombei Verdc., *Lewis* 5914 (Kenya). *P. silvatica* (K. Sch.) Bremek., *Lewis* 6049 (Tanganyika).

Pentanopsis fragans Rendle, *Ellis* 125 (K) (Ethiopia).

Pentas lanceolata (Forsk.) Deflers subsp. *lanceolata* var. *lanceolata*, *Lewis* 5928 (Kenya); subsp. *quartiniana* (A. Rich.) Verdc. var. *leucaster* (Krause) Verdc., *Lewis* 5930 (Kenya); subsp. *quartiniana* var. *oncostipula* (K. Sch.) Verdc., *Lewis* 6340 (Tanganyika). *P. pubiflora* S. Moore, *Lewis* 5963 (Kenya). *P. zanzibarica* (Klotzsch) Vatke var. *intermedia* Verdc., *Lewis* 6005 (Uganda).

Placopoda virgata Balf. f., *Bent* s. n. (K) (Socotra).

Pentodon pentandrus (Schum. & Thonn.) Vatke, *Lewis* 6055 (Tanganyika).

Pseudonesohedyotis bremekampii Tennant, *Bruce* 700 (K) (Tanganyika).

Sacosperma paniculatum (Benth.) G. Taylor, *Louis* 13166 (S) (Congo, Léop.).

Schismatoclada citrifolia (Lam. ex Poir.) Homolle, *Decary* 10444 (S) (Madagascar). *S. psychotrioides* Baker, *Baron* 189, 1769 (K) (Madagascar).

Stephanococcus crepinianus (K. Sch.) Bremek., *Louis* 2037 (K) (Congo, Léop.).

Thecorchus wauensis (Schweinf. ex Hiern) Bremek., *Adams* 3918 (K) (Ghana).